H I L G A R D I A

A Journal of Agricultural Science Published by the California Agricultural Experiment Station

VOL. 11 SEPTEMBER, 1938 No. 9

APHIDS FEEDING ON CELERY IN CALIFORNIA[1, 2]

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CONTENTS

INTRODUCTION

THE RÔLE OF APHIDS in the transmission of virus diseases of celery, *Apium graveolens* Linn., var. *dulce,* in California has attained considerable economic importance in recent years. The object of this paper is to furnish information as to the identity of the various species involved, the determination of which has been a difficult task. It has been especially complicated by the large number of different species discovered feeding on celery and by the fact that the species appear to be considerably altered, particularly in size, when reared in the greenhouse. Many of the species studied appear to be introduced, while others are undoubtedly indigenous. An abundance of wild umbelliferous plants, growing in all of the celery-producing sections of California, affords a continuous and ample food supply throughout the year. Certain of the aphids studied alternate from these hosts to willow, honeysuckle, and many other cultivated and wild plants. Carrots and celery are extensively grown as winter crops in many parts of California and aphids may be found upon them almost any time of the year. In view of the great abundance and wide distribu-

[1] Paper received for publication July 20, 1936; some notes on distribution and host range added in August, 1937.

[2] The drawings were made from funds received from the N.Y.A. and the W.P.A.

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tion of the many food plants, the commercial control of aphids to a degree that will prevent the losses to celery from the insect-borne plant virus diseases presents a most complex and difficult problem to solve.

THE CELERY LEAF APHID

Aphis apigraveolens Essig n. sp.

The celery leaf aphid, *Aphis apigraveolens* (fig. 1), a new species, was first taken on celery at Venice, California, in June, 1935, by J. H. Freitag, who subsequently propagated it in the greenhouse at Berkeley on that plant. In December of the same year he also discovered it in the commercial celery fields of Milpitas.

The specimens studied for this account have all been reared under glass and may therefore be smaller than those which occur out of doors; for many species propagated in the greenhouse here at Berkeley have proved to be much smaller than those collected in the fields. This dwarfing may also occur when transferred to different hosts, so that it has not been definitely proved whether the diminution is due to greenhouse conditions or to the influence of the host or to both.

Frequently the coloration is also markedly altered when the aphids are thus artificially reared. It is to be expected that the measurements and color pattern may prove at variance in specimens occurring in the fields and on other hosts, if such are discovered.

Apterous Viviparous Female.—Very small, elongated, somewhat depressed, and pointed posteriorly. Color pale yellow with head and anterior portion of the body amber or orange and with the tips of the appendages dusky; a series of small green patches occurs along the sides of the abdomen, a small green median patch and a prominent, somewhat bilobed green band across the abdomen on the segment in front of the cornicles. This band is similar to that of *Aphis apii* Theobald and may lead to the confusion of the two species if a microscopic examination is not made. The antennae are shorter than the body, the lengths of the segments being: I, 0.04 mm; II, 0.05 mm; III, 0.24 mm; IV, 0.11 mm; V, 0.13 mm; VI, 0.30 (base, 0.10 mm, unguis, 0.20 mm); total 0.87 mm. There are no secondary sensoria. The lateral prothoracic tubercle is prominent. The legs are short and marked as illustrated (fig. 1). The cornicles are dark, short, nearly cylindrical or slightly tapering apically, usually somewhat enlarged near the tip, with a small flange, slightly recurved in many individuals, imbricated; length 0.15 mm. The cauda is dark, upcurved, with three or four pairs of curved hairs; length 0.20 mm.

Length of body, 1.30 mm; width, 0.70 mm.

Alate Viviparous Female.—The colors of the winged individual appear black and yellowish green to the unaided eye, but a close examination reveals the head, thorax, and appendages black as illustrated in figure 1. The abdomen is yellow or very pale green with darker-green markings much as noted in the apterous individual. In addition there are small, nearly circular, dusky or black spots arranged in two laterodorsal longitudinal rows, a small median patch and two rather large, irregular, dark, lateral patches, and a transverse dark line anterior to the cauda. The antennae are

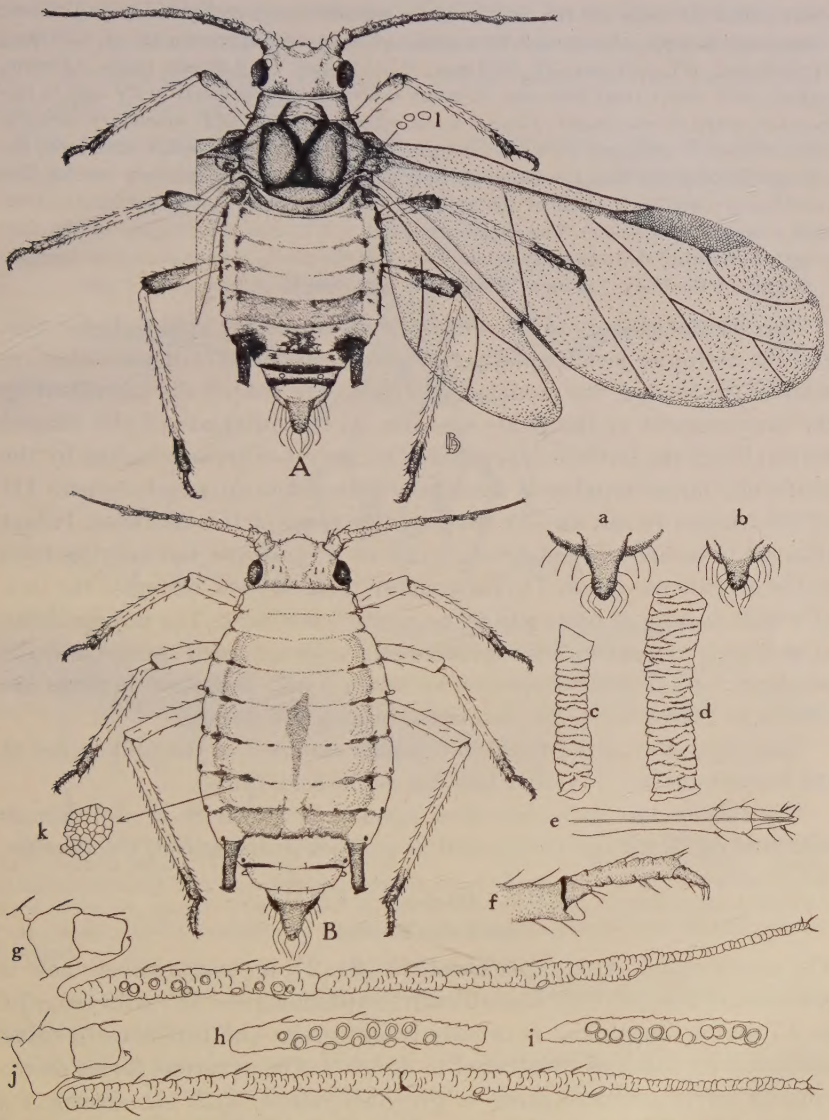

Fig. 1.—The celery leaf aphid, *Aphis apigraveolens* Essig. *A*, Adult winged female: *b*, cauda; *c*, cornicle; *g*, antenna; *h* and *i*, segment III of antennae showing different arrangements of sensoria; *l*, circular fenestras at the base of subcostal vein. *B*, Adult apterous female: *a*, cauda; *d*, cornicle; *e*, rostrum; *f*, tarsus; *j*, antenna; *k*, body reticulations; *l*, fenestras. All greatly enlarged.

shorter than the body and the lengths of the segments vary considerably in different individuals. Lengths of segments for a single average-sized specimen are: I, 0.05 mm; II, 0.06 mm; III, 0.25 mm; IV, 0.14 mm; V, 0.12 mm; VI, 0.30 mm (base, 0.10 mm, unguis, 0.20 mm); total 0.92 mm. In many individuals, V is equal to IV and in one instance noted it was longer. From 6 to 13 rather large, circular secondary sensoria are scattered or arranged in a row on segment III. Of fifty segments examined, the average number was 9.62 per segment. Only one segment had 6 and only one 13. The cornicles are similar to those of the apterous forms in color, shape, and imbrication, with a length of 0.18 mm. The length of cauda is 0.12 mm. The stigma of the fore wing is noticeably short and the second branch of the media is near the apical margin.

Length of the body, 1.25 mm; width, 0.48 mm; length of fore wing, 2 mm.

This species is likely to be confused with the celery aphid, *Aphis apii*, and the cotton or melon aphid, *Aphis gossypii*. In color it somewhat resembles the former, but mounted specimens are readily distinguished by the arrangement of the fewer sensoria on the antennae of the winged forms. From the latter it is separated by the color arrangements, by the uniformly larger number of secondary sensoria on antennal segment III of the winged forms, and by the peculiar form of the cornicles. It was thought to be one of the various forms of *A. gossypii*, but rearing tests in the greenhouse pointed to the contrary. These tests, owing to the lack of a wide variety of hosts, are by no means conclusive. The impossibility of definitely relegating this aphid to any known named species and the necessity for a definite cognomen by which it may be known in print are offered as justifications for describing it as a new species.

The celery leaf aphid feeds in compact colonies on the undersides of the leaves of celery. No other host has as yet been found.

The species has been described from a large series of individuals mounted on slides and designated as cotypes in the author's collection.

THE CELERY APHID

Aphis apii Theobald[4]

The celery aphid, *Aphis apii* Theobald (fig. 2), is comparatively new to science and is as yet little known even to aphidologists. It varies from 1.0 to 2.7 mm in length and is usually bright green and luteolous in color, marked with black as illustrated in figure 2. The apterous forms occurring on celery are pale green to greenish yellow, with blue-green or a darker-green bilobed band across the dorsum of the abdomen between and in front of the bases of the cornicles. The colors may vary somewhat in intensity, but the markings are fairly constant. The apical portion of the antennae, the tips of the tibiae, the tarsi, and the cornicles are dusky or black.

The winged forms are similar in color, but the abdomen is usually

[4] See Theobald (1925, p. 42; 1926–1929, vol. 2, p. 182–83, fig. 81).

darker green. The head and thorax are shining black. The antennae and cornicles are black and the apical portions of the femora and tibiae, and all of the tarsi are dusky. The dorsal, darker-green, bilobed band is also noticeable on the abdomen.

This species is similar to *Aphis apigraveolens* n. sp., but has less orange and yellow in the color, fewer sensoria on the third antennal seg-

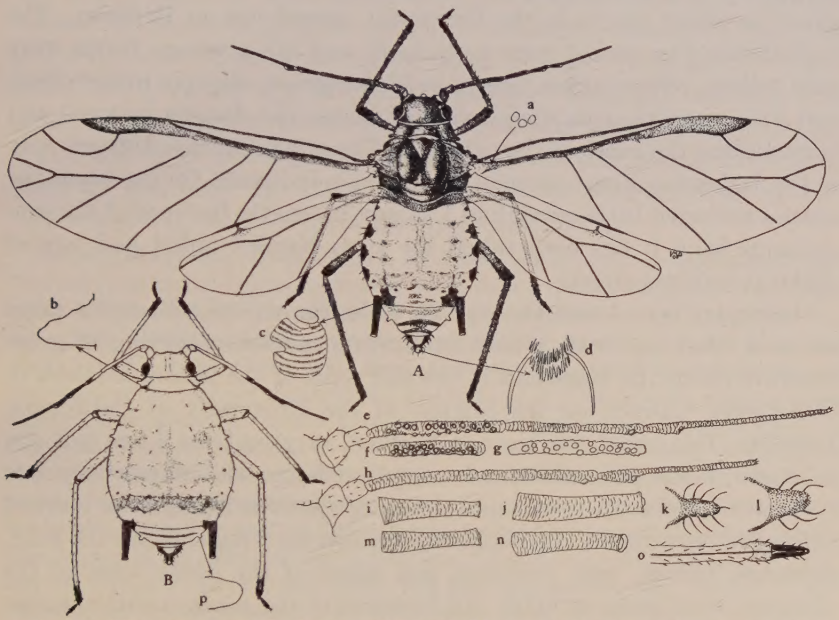

Fig. 2.—The celery aphid, *Aphis apii* Theobald. *A*, Adult winged female: *a*, fenestras; *c*, derm behind the bases of the cornicles; *d*, tip of cauda; *e*, antenna; *f* and *g*, antennal segment III, showing variation in the arrangement of the sensoria; *i* and *m*, cornicles; *k*, cauda; *o*, rostrum. *B*, Adult apterous female: *b*, prothoracic tubercle; *h*, antenna; *j* and *n*, cornicles; *l*, cauda; *p*, posterior abdominal tubercle. All greatly enlarged.

ment of the winged forms, shorter unguis of the last antennal segment, and darker cornicles.

The celery aphid occurs chiefly on the undersides of the leaves of the host plants. It has been reported from four localities in England by Theobald (1926–1929, vol. 2, p. 183).

In California the species was first discovered on shipments of celery from Gardena by H. H. P. Severin and J. H. Freitag, October 4, 1934. The next year it was noted on shipments from Compton and Venice. Severin and Freitag also collected it in the celery fields at Alviso, Chula Vista, Lomita, Malibu Beach, Milpitas, Mountain View, Palo Alto, San Fernando, and Seal Beach in 1935, and on sweet fennel, *Foeniculum*

vulgare, at Milpitas the same year. For two years they have reared it on celery in the greenhouse at Berkeley.

THE RUSTY-BANDED APHID

Aphis ferruginea-striata Essig n. sp.

In August, 1934, Severin and Freitag collected an aphid on celery in Los Angeles and Mountain View, California, which was subsequently propagated on celery plants in the University greenhouse at Berkeley. The individuals thus reared were very small and the apterous forms were pale yellow, yellow-amber, green, or bluish green, slightly pulverulent, and with a conspicuous rusty-red band across the dorsum between and surrounding the bases of the cornicles. The winged forms differed only in the darker markings common to winged individuals. On the whole the species averaged little more than 1.25 mm in length. Because of the conspicuous band it has been called the rusty-banded aphid and named *Aphis ferruginea-striata.*

On September 14 and October 24, 1934, the writer collected a large series of what was truly a most interesting species, occurring in great numbers about the bases and in the leaf axils of the poison hemlock in Strawberry Canyon on the campus of the University of California, Berkeley. This aphid was large and robust, varying from 2 mm to 3 mm in length; it was pale amber and covered with fine whitish powdery wax that gave a decidedly gray aspect. Mature apterous forms were marked with a few dorsal spots and bands, whereas on the winged forms the head, antennae, thorax, legs, cornicles, and much of the dorsal area of the abdomen were dusky or black. All forms were also marked with the conspicuous rusty band which at once suggested that it might be identical with the species previously found feeding on celery by Severin and Freitag, and it is so considered in this paper.

The naming of this species presented many difficulties and a perusal of the literature did not reveal a solution to the problem. At first it was thought to be *Rhopalosiphum foeniculi* (Passerini), reported by Davidson (1910, p. 377) on the sweet fennel in the vicinity of Stanford University, California, in November, 1909, but no adequate description was given, and specimens have not been examined. This supposition was further strengthened by the fact that Theobald (1926–1929, vol. 2, p. 77–78), in referring to this species, makes this significant statement: "Passerini remarks that the alate female is sometimes rusty between the cornicles." This rusty band, together with the somewhat swollen cornicles, might seem to justify the above determination. However, in order to avoid a possible mistake, specimens were sent to specialists in America and in Europe, but without beneficial results.

On July 23, 1936, the writer discovered an aphid at the bases of the stalks, near and even under the surface of the ground, and in the leaf axils of the common wild parsnip, growing abundantly along the roadside near Newmarket, England. The species looked like the one taken on poison hemlock in California, with the exception that the rusty band was absent, but the size, shape, and habits appeared almost identical; and it was also attended by ants, which covered certain of the aphids near the bases of the plants in a similar manner. This English species was mounted and was identified as *Aphis subterranea* Walker (*Anuraphis*) (Theobald, 1926–1929, vol. 2, p. 277–81, figs. 128–30). Naturally the California species was thought to be this one and specimens of the latter were sent for. While there are important resemblances in size, shape, and habits, there are also some important differences which seem sufficient to warrant describing the California aphid as a new species.

Apterous viviparous female. (Fig. 3, *B*). Large, robust, slow-moving species. Color varying from amber to grayish brown, often with a reddish tinge, and with many small dark markings, as shown in the accompanying illustration (fig. 3, *B*). The eyes, legs, portions of the antennae, the cornicles, cauda, and anal plate are dusky. In the living forms there is a conspicuous rusty-red band between and surrounding the bases of the cornicles. The bodies are often covered with a whitish pulverulence, giving a decided grayish or frosted appearance. There is a pair of conspicuous lateral tubercles on the prothorax and pairs of smaller tubercles on the sides of most of the abdominal segments, and on the dorsum of the head, prothorax, and the 8th abdominal segment. The antennae are much less than half the length of the body and are dusky, except the base of segment III, which is pale. The lengths of the segments are: I, 0.07 mm; II, 0.06 mm; III, 0.32 mm; IV, 0.21 mm; V, 0.14 mm; VI, 0.37 mm (base, 0.08 mm; unguis, 0.29 mm); total 1.17 mm. There are no secondary sensoria on the antennae of any of the specimens examined. The rostrum extends to or slightly beyond the 2d coxae. The cornicles are very finely imbricated, dusky, widest at the base and nearly cylindrical, with the apical portion constricted and terminating in a flange which has a diameter smaller than that of the base. In some specimens these organs are somewhat swollen in the middle. The length is 0.25 mm; the width 0.05 mm. The cauda is rounded and about twice as broad as long. The anal plate is almost hemispherical and much wider than the base of the cauda.

Length of the body: 2.75 mm; width, 1.14 mm.

Alate viviparous female (fig. 3, *A*). The general color is the same as that of the apterous form, but much darker. The head and thoracic regions, eyes, antennae, legs, cornicles, cauda, anal plate, and the lateral and dorsal abdominal patches are all dusky or black as shown in figure 3, *A*. In cleared, mounted specimens, the apical portions of the cornicles appear paler than the bases. The antennae are considerably shorter than the body. The lengths of the segments are: I, 0.07 mm; II, 0.06 mm; III, 0.47 mm; IV, 0.28 mm; V, 0.15 mm; VI, 0.50 mm (base, 0.10 mm; unguis, 0.40 mm); total, 1.53 mm. Numerous circular secondary sensoria occur on the segments as follows: III, 64 to 75; IV, 13 to 26; and V, usually none, but rarely with 1 to 5. The sensoria are so crowded over the whole of segment III that they are extremely

difficult to count, so that these figures are only approximately correct. The fore wings are much longer than the body and have a well-defined stigma and strongly curved stigmal vein; the second branch of the media arises from about the middle of that vein. The cornicles are similar to those of the apterous forms, but are more constricted at the bases and somewhat swollen in the middle and terminate in a conspicuous

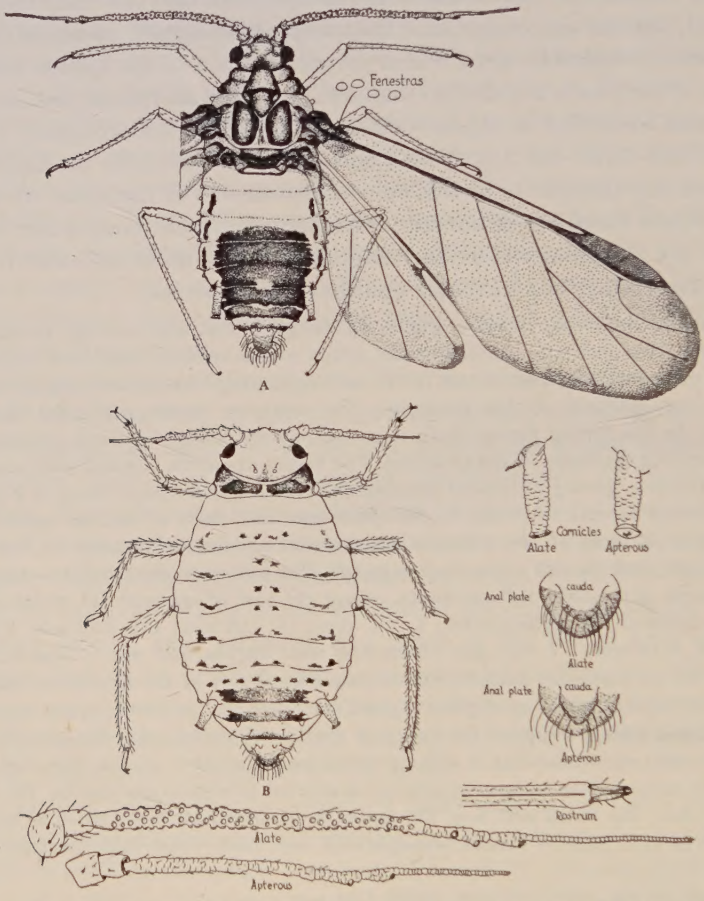

Fig. 3.—The rusty-banded aphid, *Aphis ferruginea-striata* Essig. *A*, Adult winged female; *B*, adult apterous female. Other parts are labeled. All greatly enlarged.

flange. The length is 0.24 mm; width, 0.04 mm. The cauda is longer than wide and approximately one-half the length of the cornicle. The anal plate is nearly twice the width of the base of the cauda and about the same length.

Length of body, 2.0 mm; width, 0.9 mm; length of fore wing, 3.3 mm.

Because of the small size of the specimens reared on celery in the greenhouse, the descriptions have been made from aphids taken on the

poison hemlock. The greenhouse forms on celery agree rather well in general characteristics, but are only about one-half as large and may have slightly fewer sensoria on the very small antennal segments of the winged forms.

Aphis ferruginea-striata n. sp. is perhaps nearest to *Aphis subterranea* Walker, but differs most strikingly in the absence of secondary sensoria on the antennae of the apterous forms, in having longer cornicles, somewhat shorter rostrum, and the presence of the rusty-red band in the living forms.

The description has been made from a large series of individuals mounted on slides and designated as cotypes in the collection of the author and those of several of his students.

According to Börner and Schilder (1932), *Aphis heraclei* Koch is a synonym of *A. subterranea* Walker. Specimens labeled *A. heraclei* Koch in the British Museum of Natural History are not at all like *A. subterranea* Walker. Attention should also be called to the fact that both *A. ferruginea-striata* and *A. subterranea* bear considerable resemblance in appearance and habits to *A. lappae* Koch, as described and figured by that author (Koch, 1854–1857, Heft 2. p. 50). His description, which is worthy of note, is as follows: "*Sie bewohnt die Klette* [burdock] *und hält sich nahe, auch etwas unter der Erde an den Achseln der Blattstiele der jungen Pflanzen auf. Man findet sie in grössern und kleinern Kolonien dicht beisammen sitzend.*" Since burdock is not closely related to the umbelliferous hosts of *Aphis ferruginea-striata* and *A. subterranea*, Koch's species may not be so closely allied as the description would seem to indicate. *Aphis angelicae* Koch, occurring on *Angelica sylvestris* in Europe, is also very closely related to all three of these species, but the exact relations of this particular aphid complex cannot be settled until Koch's species have been definitely established and comparisons made with them and possibly with other species also.

The known host and locality records are as follows:

Anise or dill, *Anethum graveolens*—Berkeley, California, by Essig and W. D. Riley
Carrot—North Sacramento, California, by J. E. Spurlock; Europe
Celery—Los Angeles, Berkeley, Mountain View, California, by Severin and Freitag
Sweet fennel, *Foeniculum vulgare*—Berkeley, California, by Essig; Milpitas, California, by Freitag; Palo Alto, California, by W. M. Davidson; Europe
Parsnip—Europe
Parsley—Keyes, California, by Severin
Poison hemlock, *Conium maculatum*—Milpitas and Alviso, California, by Severin and Freitag; Berkeley, California, by Essig; Europe

Severin and Freitag report collections of this species on celery plants in the celery-producing districts near Alviso, Chula Vista, Compton,

Lomita, Long Beach, Malibu Beach, Milpitas, Mountain View, Palo Alto, Redwood City, Seal Beach, Walteria, and West Sacramento. They have also taken it in celery shipments from Gardena and Venice.

On celery plants the aphids usually occur between the petioles near the base, sometimes below the surface of the soil. But when abundant they may also feed on the petioles and blades of the plants.

Colonies of aphids feeding about the bases of the plants in the fields are often partially covered with minute particles of soil by attending ants.

THE COTTON OR MELON APHID

Aphis gossypii Glover

The cotton or melon aphid, *Aphis gossypii* Glover (fig. 4), has been a serious pest in this country since its discovery by Townend Glover in 1854. At first it was chiefly known as a cotton pest, but as knowledge about aphids accumulated, it was found to be an omnivorous feeder and a ravager of many crops. It is a relatively small species scarcely more than 1–2 mm long; on certain hosts like *Sedum* spp., growing in the open, and on celery raised in greenhouses, it may be scarcely half as large. In color it is variable. Some forms taken on catalpa in Fresno and on celery in the greenhouse at Berkeley are very yellow, whereas the normal color varies from yellowish green to dark olive-green or almost dull black. The apterous forms are usually somewhat mottled. The winged forms have dusky or black head, thorax, and cornicles, whereas most of the antennae and legs are pale. Specimens of what have been determined as this species, from many parts of the world, show an interesting variation in the number, size, and arrangement of the secondary sensoria on segment III of the antennae, as well as some marked differences in the cornicles and the cauda as shown in figure 4. Whether these differences represent mere variants or actually separate species has not yet been determined, but careful studies might well be made to determine more exactly the causes for such wide differentiation in this particular species.

The life history of this aphid in the cultivated areas of California appears to be very simple. Winged and apterous parthenogenetic viviparous females occur throughout the year. No true sexual forms have been observed here. During the winter months, propagation is slow, but as spring advances the aphids become numerous, and by summer they are scattered far and wide over all the fields and orchards. The winged migrants are carried by the prevailing winds for long distances so that newly planted crops are infested almost as soon as the plants appear above ground.

The cotton aphid is almost as omnivorous in its food habits as the green

peach aphid and accordingly attacks a long list of a wide variety of hosts[5] of which the following are the most important: amaranthus, asparagus, avocado, beans, beets, burdock, cantaloupe, catalpa, celery, *Cheno-*

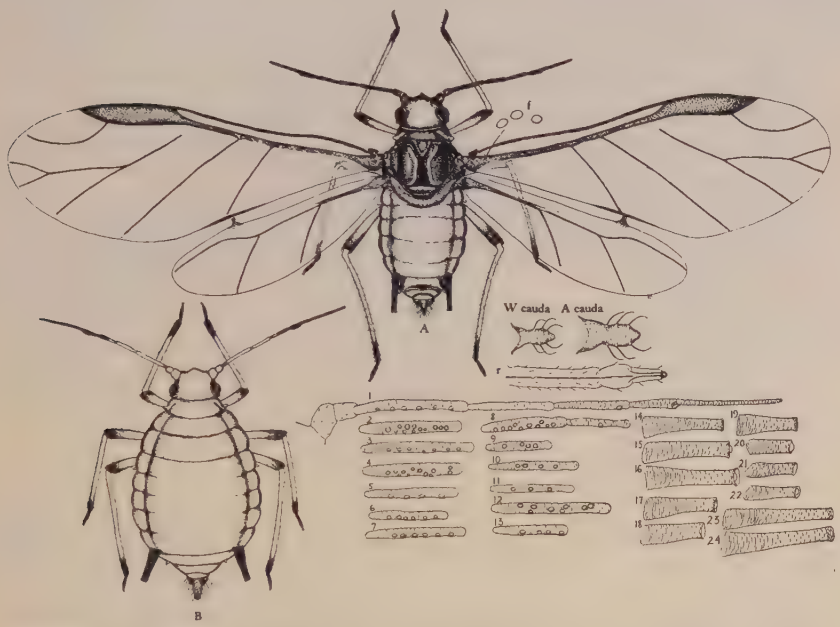

Fig. 4.—The cotton or melon aphid, *Aphis gossypii* Glover. *A*, Winged viviparous female; *B*, apterous viviparous female; *W cauda*, cauda of winged female; *A cauda*, cauda of apterous female; *f*, fenestras; *r*, rostrum. *1*, Antenna of winged female on cotton, California. *2–13*, Antennal segment III of winged female drawn to scale to show variation in number of secondary sensoria, and length: *2*, on orange, California; *3*, on cotton, California; *4*, on cantaloupe, California; *5*, on *Rhamnus*, California; *6*, on sour sop, Florida; *7*, on unnamed host, Japan; *8*, on citrus, California; *9*, on cotton, Mississippi; *10*, on elm, New York; *11*, on cotton, China; *12*, on *Bidens*, South Rhodesia; *13*, on cucurb, India; *14–24*, types of cornicles drawn to same scale and showing variation to be found in the winged individuals: *14*, on cotton, China; *15*, on *Bidens*, South Rhodesia; *16*, on milkweed, California; *17*, on *Leucopis*, California; *18*, on *Rhamnus*, California; *19*, on elm, New York; *20*, Japan; *21*, cineraria, California; *22*, on gardenia, Florida; *23*, California; *24*, on cotton, California. Antennal segment III as represented by *5*, *9*, *10*, *11*, and *13*, appear identical with those in the European species *Aphis sedi* Kaltenbach, which also occurs in California. All greatly enlarged.

podium, chrysanthemum, cineraria, citrus (grapefruit, lemon, orange, etc.), clover, coprosma, cotton, cucumber, dandelion, *Datura*, dock, dog-

[5] The most important lists of host plants are to be found as follows: J. Davidson (1925, p. 36); Essig (1911, p. 338–39; 1924, p. 241–42); Hall (1926, p. 19); Mimeur (1934, p. 29–30); Smith (1934, p. 115); Gillette and Palmer (1931–1934, vol. 25, p. 401); Swain (1919, p. 106); Takahashi (1921–1931, pt. 6, p. 6–13); Theobald (1926–1929, vol. 2, p. 144); Wilson and Vickery (1918, p. 84).

wood, *Echeveria*, eggplant, filaree, fuchsia, gardenia, hibiscus, hop, hydrangea, lilies, malva, milkweed, morning-glory, onion, pear, phacelia, plantain, poppy, portulaca, potato, pumpkin, Russian thistle, *Sedum*, shepherd's-purse, spinach, squash, strawberry, thistles, tomato, vetch, violet, and watermelon.

The members of this species usually occur in rather dense, and often very extensive, colonies and at times may completely cover and destroy the hosts. For this reason it has been found desirable to destroy the foci of early infestations to prevent subsequent spread in the case of cucurbits and some other cultivated crops.

This aphid is widely distributed throughout many parts of the world and has been definitely reported to occur in the following regions and countries:

Africa: Algeria, Anglo-Egyptian Sudan, Belgian Congo, British Togoland, Portuguese East Africa, Egypt, Eritrea, French West Africa, Italian Somaliland, Morocco, Nigeria, Nyasaland, Rhodesia, South Africa, Tanganyika Territory, and Uganda.

Asia: Armenia, Asiatic Russia, Astrakhan, Ceylon, China, Formosa, India, Japan, Malaya, Pescadores Islands, Transcaucasia, and Turkistan.

Europe: Crimea, Cyprus, Denmark, Germany, Great Britain, Italy, U. S. S. R., and Sweden.

North America: Bermuda, Canada, Central America, Mexico, United States, West Indies.

South America: Argentina, Brazil, British Guiana, Chile, Dutch Guiana, Paraguay, Peru.

Oceania and the Pacific: Australia, Dutch East Indies, Fiji, Hawaii, Philippine Islands, and Samoa.

In the United States this aphid appears to occur in practically every state, having been reported from every important geographical region within the country.

In California it is to be found abundantly from the Imperial Valley and San Diego to Oregon. In the warmer valleys—Imperial, San Fernando, San Joaquin, Salinas, and Sacramento—it may become exceedingly abundant and destructive, especially to melons and cotton in the spring and early summer.

THE COW PARSNIP APHID

Aphis heraclella Davis
(*Aphis heraclei* Cowen)[9]

The cow parsnip aphid, *Aphis heraclella* Davis (fig. 5), is medium-sized and dark green, often mottled with paler green or yellow, with dusky lateral and dorsal areas on the posterior dorsum of the abdomen; and the an-

[9] Since the name *Aphis heraclei* Cowen was preoccupied by the European species *Aphis heraclei* Koch 1854, the species was renamed *Aphis heraclella* by Davis (1919).

tennae, cornicles, cauda, and the greater part of the legs are dusky. The head and thorax of the winged forms are black, and there are more dorsal abdominal black patches in these forms than in the apterous forms. On the whole the species appears very dark olive-green or blackish. It is further characterized by the numerous sensoria on antennal segment III of the alates and by cylindrical or tapering cornicles, which are closely imbricated and flanged at the openings.

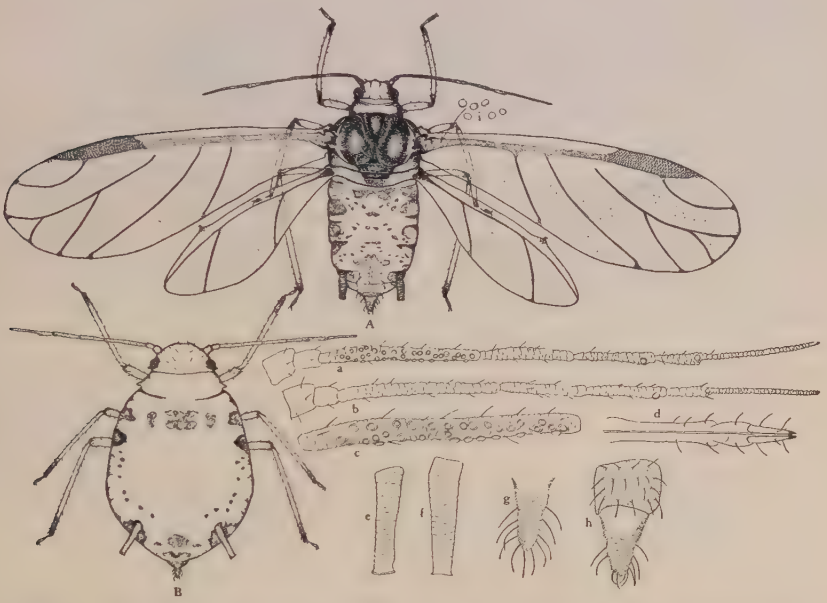

Fig. 5.—The cow parsnip aphid, *Aphis heraclella* Davis. *A*, Adult winged female: *a*, antenna; *c*, antennal segment III; *g*, cauda; *i*, fenestras. *B*, Adult apterous female: *b*, antenna; *d*, rostrum; *f*, cornicle; *h*, anal plate and cauda. All greatly enlarged.

This species was originally taken on cow parsnip at Fort Collins and described as *Aphis heraclei* by Cowen in 1895 (Gillette and Baker, 1895, p. 120). Gillette and Palmer (1931–1934, vol. 25, p. 406) have redescribed this species and state that it is "structurally indistinguishable from *A. helianthi* unless an apparent tendency to longer antennal joints and cornicles and darker-green coloration can be considered of sufficient value for separation." Specimens collected on cow parsnip in California and Oregon and a small series from San Diego, California, on celery agree very well with the sunflower aphid, *A. helianthi* Monell.[7] This dis-

[7] For a good description and illustrations of this species see Gillette and Palmer (1931–1934, vol. 25, p. 402–4).

cussion, however, involves only the so-called *A. heraclella* Davis. As such it has been reported on the following hosts in the West:

Angelica tomentosa—Berkeley, California, by Essig
Celery—Colorado, by Gillette and Palmer; San Diego, California, by Essig
Cow parsnip, *Heracleum lanatum*—Colorado, by Cowen, Gillette and Palmer; Multnomah Falls, Oregon, by Essig
Heracleum Mantegazzianum—Berkeley, California, by Essig
Parsnip—Colorado, by Gillette and Palmer
Umbelliferous plant—Scott's Valley, Lake County, California, by P. S. Schulthess
Water-hemlock, *Cicuta occidentalis*—Colorado, by Gillette and Palmer

So far it has been observed only once on celery in California.

THE ERIGERON ROOT APHID

Aphis middletonii Thomas[8]

For many years an aphid has been taken in considerable numbers on the roots of cultivated asters and a wide range of other plants in California. The species bears a close resemblance to the common corn root aphid, *Aphis maidi-radicis* Forbes,[9] of the middle and eastern states, but has so far not been identified as that species. Rather it appears to agree more closely with the form described as *Aphis middletonii* by Thomas in 1879 (Thomas, 1879) and is commonly called the erigeron root aphid (fig. 6). Specimens of what now appear to be this species were first collected by the author on the leaves of mule fat, *Baccharis viminea*, at Santa Paula, California, August 15, 1911. No winged forms were taken, but the apterous specimens check with the species under consideration. Both winged and apterous forms were later taken in the same general area on the roots of cultivated China aster, *Callistephus hortensis*, and rough pigweed, *Amaranthus retroflexus*, on October 20, 1911. It was noted that the aster plants were seriously injured even though the aphid was very heavily parasitized by *Lysiphlebus testaceipes* (Cresson).

This aphid is first recognized by its subterranean and semisubterranean habits. It is primarily a root feeder, although it also occurs at the bases of the plants near the surface of the soil in greenhouses, as well as out of doors, and has been taken on the stems and foliage above the ground. It is normally yellowish green or dark olive-green, often with a frosted or pulverulent covering. This pulverulence is usually arranged like a network consisting of small 5-sided figures or reticulations. Mounted specimens rarely reveal these as fine lines on the exoskeleton;

[8] The more important descriptions of this aphid are those of Thomas (1879, p. 99); Gillette and Palmer (1931–1934, vol. 25, p. 418–20); Oestlund (1887, p. 54–55); Swain (1919, p. 115–16); Vickery (1910, p. 113–18); and Williams (1910, p. 51–52).

[9] The confusion concerning this species and *Aphis middletonii* Thomas have been discussed by Vickery (1910) and by Hottes and Frison (1931, p. 203).

if stained, however, they show the network well. They are characteristic of the species and aid in its identification. The subterranean and greenhouse forms are much paler than those occurring out of doors about the bases of the plants. Mounted specimens are characterized by arrangement of the sensoria on the antennae of both the winged and apterous

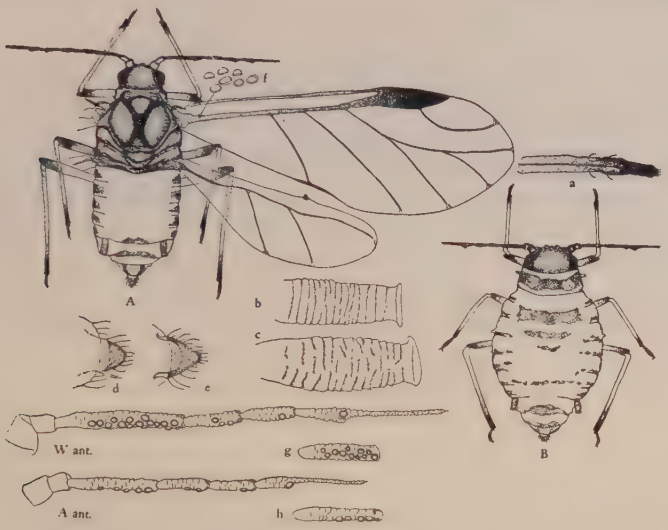

Fig. 6.—The erigeron root aphid, *Aphis middletonii* Thomas. *A*, Adult winged female: *W ant.*, antenna; *a*, rostrum; *b*, cornicle; *d*, cauda; *f*, fenestras; *g*, antennal segment III. *B*, Adult apterous female: *A ant.*, antenna; *c*, cornicle; *e*, cauda; *h*, antennal segment III. All greatly enlarged.

forms, by the rather short spur or unguis of the apical antennal segment, and by the short and cylindrical cornicles.

The erigeron root aphid has a rather scattered known distribution in North America. It has been reported from the states of California, Colorado, Illinois, Kansas, Minnesota, New York, North Carolina, North Dakota, Oklahoma, South Carolina, and Virginia. This range will undoubtedly be greatly extended as the insect becomes better known.

In California it has been taken by the writer in Ventura and Alameda counties, by R. R. McLean in San Diego County, by A. F. Swain in Riverside and Santa Clara counties, and by Severin and Freitag in Santa Clara and San Diego counties.

The host range of the erigeron root aphid is very extensive and, including hosts from all sources, is as follows: *Artemisia frigida,* artichoke (*Cynara Scolymus*), *Aster multiflorus, Aster subulatus,* avocado (above-

ground), bristly oxtongue, California buttercup, celery (aboveground), China aster, corn, cosmos, dahlia (?), daisy fleabane (*Erigeron ramosus*), dandelion, fleabane, flixweed, goldenrod, *Helianthus pumilus*, horseradish, horseweed, milkweed, mule fat (aboveground), naked broom rape, ragweed, rough pigweed, *Senecio*, sheep sorrel, shepherd's-purse, sunflower, and tarweed.

THE YELLOW WILLOW APHID

Cavariella capreae (Fabricius)[10]
(*Aphis capreae* Fabricius)

The yellow willow aphid, *Cavariella capreae* (Fabricius) (fig. 7), an Old World species, has now attained a rather wide distribution throughout the temperate regions and is an economic pest of considerable importance, especially on a number of the umbelliferous plants, although the primary host consists of various species of willow.

The general color is yellow of varying shades, but individuals or whole colonies may be distinctly green. The apterous forms are usually immaculate. The winged forms are marked with black as shown in figure 7. The most characteristic features of this aphid are: the dorsal tubercle at the posterior end of the abdomen above the cauda, which in the apterous forms is a pointed prolongation of the abdomen, and in the alates a very small tubercle, scarcely noticeable; the short unguis of the last antennal segment; and the somewhat swollen cornicles, which are rather like those of the green peach aphid.[11]

This species has been reported from Denmark, France, Belgium, Germany, Great Britain, Holland, Latvia, and Sweden in Europe; in Argentina, South America; and in the United States. In this country it probably has a much wider distribution than the published records indicate because it has so often been confused with other closely related species. In Colorado and California it is well known in a number of localities. In California it was first reported from willow at Berkeley by W. T. Clarke in 1903. Since then it has been taken on that host in many localities from San Diego to Newcastle. Severin and Freitag first took it from celery in shipments from Gardena, Lomita, and Venice in 1935. During that year they either collected it in the celery fields of or in shipments from Bassett, Chula Vista, Compton, Costa Mesa, East Whittier, Hawthorne, Malibu

[10] This aphid has been referred to the genera *Hyadaphis*, *Rhopalosiphum*, and *Siphocoryne* and has often been confused with a related species, *Cavariella pastinacae* (Linn.), which has also been treated under the various generic terms listed above.

[11] More complete descriptions of the yellow willow aphid may be found in the works of Gillette (1918, p. 93–94), Gillette and Palmer (1931–1934, vol. 25, p. 466–67), and Theobald (1926–1929, vol. 2, p. 5–10).

Beach, Moneta, Montalvo, Mountain View, Rosecrans, San Fernando, Santa Ana, Sawtelle, Seal Beach, Talbert, and Walteria.

The yellow willow aphid feeds chiefly on willows and umbelliferous plants. The more important hosts are: *Angelica* spp., anise or dill (*Anethum graveolens*), *Apium nodiflorum*, *Archangelica officinalis*, *Berula*

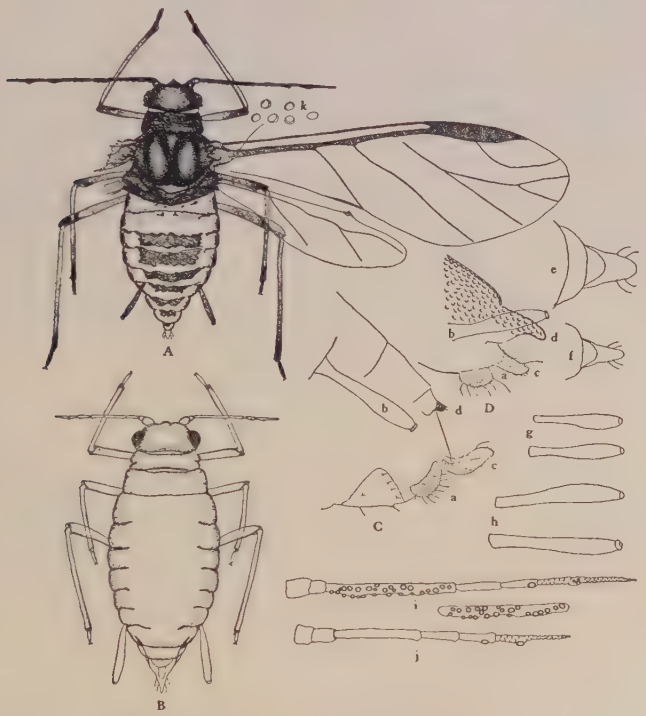

Fig. 7.—The yellow willow aphid, *Cavariella capreae* (Fabricius). *A*, Adult winged female: *e*, cauda; *g*, cornicles; *i*, antenna, *k*, fenestras at base of subcostal vein. *B*, Adult apterous female: *f*, cauda; *h*, cornicles; *j*, antenna. *C* and *D*, Posterior end of abdomen, *C* of winged, and *D* of apterous female: *a*, anal plate; *b*, cornicle; *c*, cauda; *d*, dorsal caudal tubercle. All greatly enlarged.

erecta, carrot, *Carum* spp., celery, *Chaerophyllum* spp., *Cicuta* spp., *Coreopsis* sp., cow parsnip, goutweed (*Aegopodium Podograria*), *Heracleum Spondylium*, *Ligusticum Porteri*, *Liatris* sp., parsley, parsnip, *Peucedanum* spp., and willows. In northern Europe, this aphid is widely distributed on willow and is found in the floral heads of the common wild parsnip along the highways, especially in England. *Aphis subterranea* Walker, a species not found in North America, may also occur on wild parsnip in Europe.

THE LILY APHID[12]

Myzus circumflexus (Buckton)
(*Siphonophora circumflexa* Buckton)[13]
(*Myzus vincae* Gillette)[14]

The lily aphid, *Myzus circumflexus* (Buckton) (fig. 8), is next to the green peach aphid in importance in northern Europe as a vector of plant virus diseases. It was introduced into the United States and Argentina and according to Davis (1914, p. 121) it "was first reported in this country by Mr. F. A. Sirrine" in New York, where it has become very widely distributed.

It is a rather large, robust, pale-green or yellow aphid, the apterous forms immaculate or with distinct dark markings on the dorsum as illustrated, and the winged forms with a considerable portion of the body black. The dark dorsal patches on the abdomen and the rather short, smooth, black-tipped cornicles are good superficial diagnostic characters. The lily aphid is most likely to be confused with the foxglove aphid, which it very much resembles in color and markings, but from which it may be distinguished by the dorsal markings of the apterous forms and the shorter cornicles, which lack the apical reticulations so pronounced in the foxglove aphid. Figure 8 will serve to separate mounted specimens.

The general distribution of the lily aphid includes Belgium, Great Britain and Ireland, Latvia, Sweden, Switzerland, and northern Europe generally, United States, Argentina, Hawaii, Morocco, and Sumatra.

In the United States it has been reported in California, Colorado, Connecticut, Illinois, Kansas, New York, Oregon, and South Dakota, but it probably has a much wider distribution.

In California it has been collected in the following places: Berkeley, by Essig, A. F. Swain, G. O. Shinji, Freitag, Severin, and K. Wilson; Los Angeles, by A. F. Swain; Pomona, by Essig; San Diego, by A. F. Swain; San Francisco, by G. O. Shinji and E. Walther; Stanford University, by W. M. Davidson, H. Morrison, and A. F. Swain.

The lily aphid, while it shows a fondness for liliaceous plants, is an omnivorous feeder, and attacks a wide variety of hosts. It usually occurs

[12] The more important references to literature on this species are: J. Davidson (1925, p. 21–22), Davis (1914, p. 121–22), Essig (1924, p. 252), Gillette (1908, p. 19–20, pl. I, figs. 4–8), Gillette and Palmer (1931–1934, vol. 27, p. 202, fig. 289), Hottes and Frison (1931, p. 335–36), Mimeur (1934, p. 38–39), Smith (1934, p. 111, fig. 16), Swain (1919, p. 74–75, fig. 175), Theobald (1926–1929, vol. 1, p. 331–34, fig. 177), Werder (1931, p. 52), and Wilson and Vickery (1918, p. 57).

[13] See Buckton (1876–1883, vol. 1, p. 130–32, pl. XIII).

[14] See Gillette (1908, p. 19–20, pl. I, figs. 4–8).

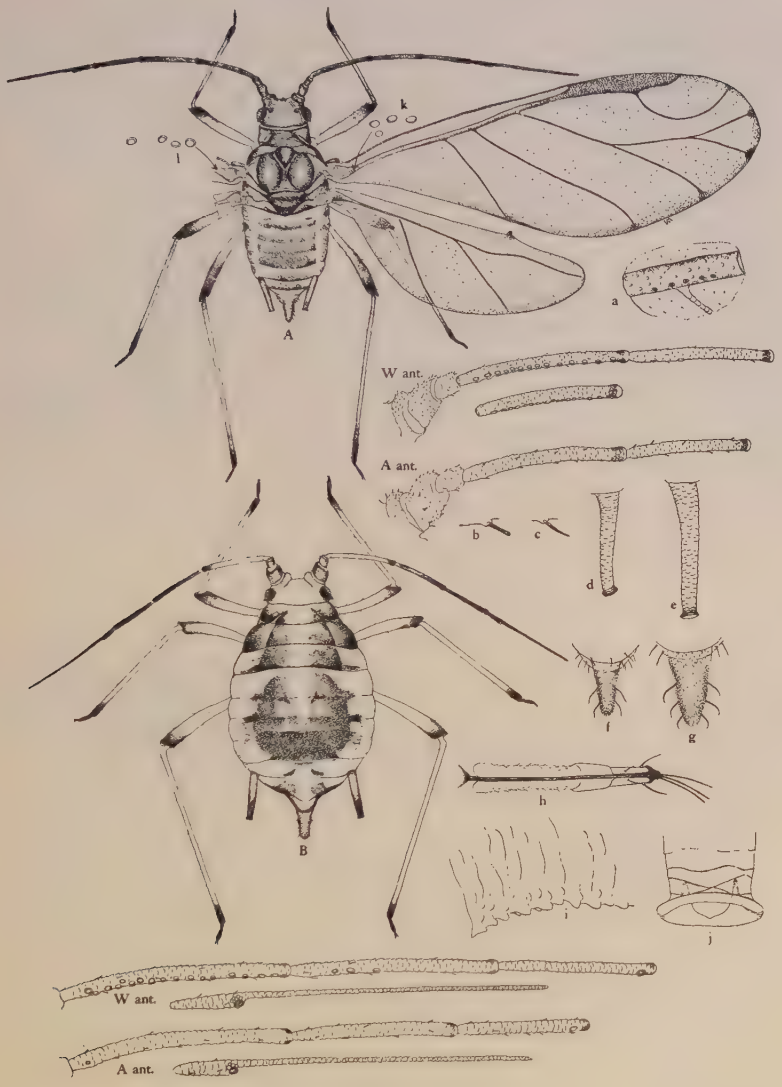

Fig. 8.—The lily aphid, *Myzus circumflexus* (Buckton). *A*, Adult winged female: *a*, section of the costal vein showing fenestralike areas; *d*, cornicle; *f*, cauda; *k* and *l*, fenestras near the base of the subcostal vein; *W ant.*, antennae. *B*, Adult apterous female: *A ant.*, antennae; *b* and *c*, setas on segments I and III of antenna; *e*, cornicle; *g*, cauda; *h*, rostrum; *i*, basal margin of cornicle; *j*, tip of cornicle. All greatly enlarged.

in dense colonies on the leaves and tender tips and may do considerable damage to the host. The following list of food plants, although extensive, is by no means complete, but it will serve to give some idea of the wide range which the species attacks: alisma, *Alopecurus,* anemone, *Antholyza refracta, Anthurium, Artemisia, Arum,* asparagus, aster, barley, California buckeye, California laurel, calla, ceanothus, celery, *Cerastium,* cineraria, clover, columbine, crocus, currant, cyclamen, dahlia, dock, elder, fig, foxglove, freesia, fuchsia, geranium, gladiolus (corms), golden glow, goldenrod, hedge mustard, horse bean, iris, marsh pennywort (*Hydrocotyle prolifera*), lilies (many kinds), *Lycium,* maidenhair fern, meadow foxtail, nasturtium, nightshade, oats, *Orchis,* oxalis, pansy, pentstemon, persimmon, *Physalis peruviana,* plantain, *Polymnia,* potato, ranunculus, schizanthus, senecio, sisymbrium, snowberry, sparaxis, spiraea, stachys, *Steironema,* thistle, tobacco, tomato, tulip, *Vinca,* violet, Virginia creeper, wallflower, watercress, and watsonia.

THE FOXGLOVE APHID

Myzus convolvuli (Kaltenbach)[15]
(*Myzus pseudosolani* Theobald)[16]
(*Macrosiphum solani* Theobald)[17]
(*Macrosiphum aucubae* Bartholomew)[18]

The foxglove aphid, *Myzus convolvuli* (Kaltenbach) (figs. 9, 10), an unusual species, appears to be entering upon a career of synonymy similar to that of the green peach aphid and the potato aphid. Perhaps the confusion concerning its identity is due to its comparatively recent appearance in the field of economic entomology, its wide host range, and its

[15] This species has heretofore been generally known as *Myzus pseudosolani* Theobald, which is now considered to be a synonym of it. The writer has also examined at the British Museum of Natural History specimens of *M. pseudolamii* Theobald and *M. mercurialis* Theobald and is in agreement with Frederick Laing in considering them also to be synonyms of *M. convolvuli* Kalt. *M. caledonii* Kalt., as described by Theobald, is also very near, but not yet positively fixed as a synonym. *M. duffieldii* Theobald is considered to be distinct by Laing.

Theobald (1926–1929, vol. 3, p. 338) relegated his *Myzus pseudosolani* to a synonym of *M. solani* (Kalt.), to which Hille Ris Lambers (1933–1934, vol. 2) agreed. The latter author also placed *M. convolvuli* (Kalt.) as a synonym of *M. solani* (Kalt.), both in the genus *Aulacorthum.* Börner and Schilder (1932, p. 628) have offered the following synonymy: "*M.* (spelled *Macrosiphon* in text) *convolvuli* Kalt. (*vincae* Walk., *solani* Kalt., *pseudosolani* Theobald)."

If this idea is accepted, then *M. solani* (Kalt.) (Kaltenbach, 1843, p. 15, *Aphis*) should have priority over *M. convolvuli* (Kalt.) (Kaltenbach, 1843, p. 40–41, *Aphis*) because the former preceded the latter in the pagination. Neither of these Kaltenbach species are now positively known.

[16] Theobald (1922*a*, p. 8, figs. 6–7).

[17] Theobald (1913, pt. II, p. 127–28, fig. 39; 1926, p. 313–15, figs. 164–65); Smith (1934, p. 112, fig. 18).

[18] Bartholomew (1932, p. 723–25, pl. II, figs. 17–20).

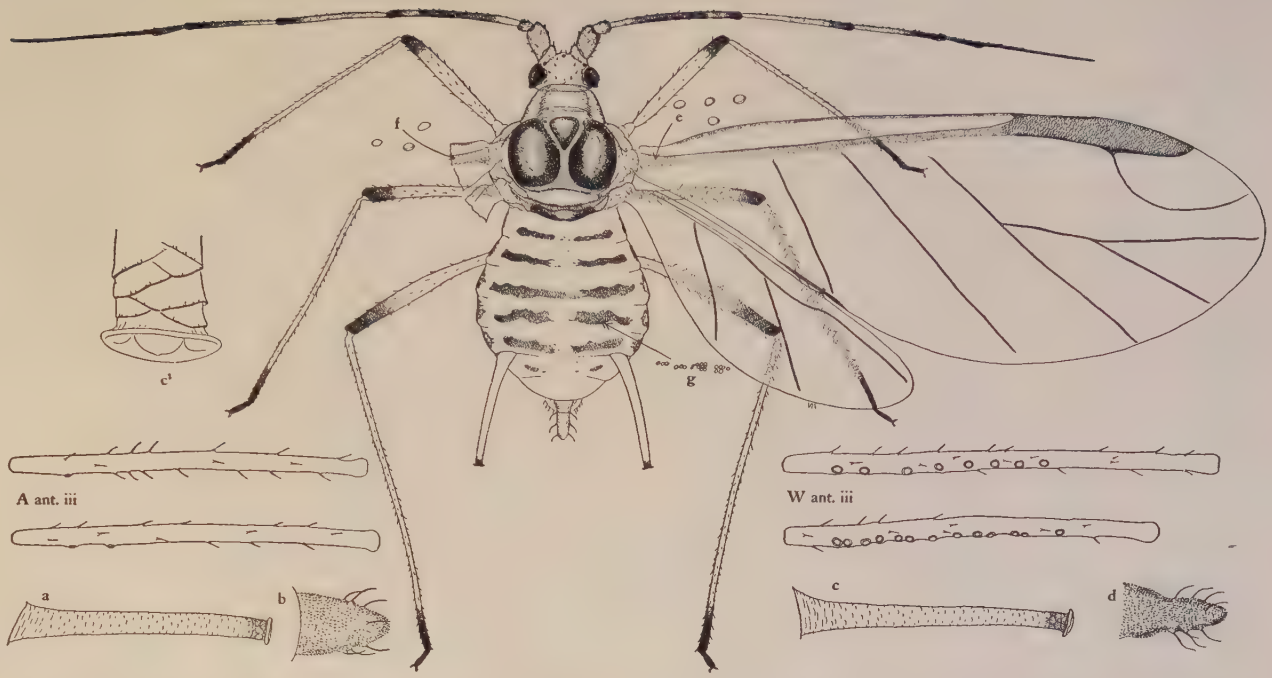

Fig. 9.—The foxglove aphid, *Myzus convolvuli* (Kaltenbach), adult winged female: *W ant.*, antennal segment III; *c*, cornicle, c^1, tip of cornicle; *d*, cauda; *e* and *f*, fenestras; *g*, gland pores as arranged in the dark transverse bands on the dorsum of the abdomen. *A ant.*, antennal segment III of apterous female; *a*, cornicle of apterous female; *b*, cauda of apterous female.

similarity to the lily aphid and related species. Although described as *Myzus psuedosolani* by Theobald in 1922, this species had first been considered by him to be *Macrosiphum solani* from its habit of feeding on the potato. Since its first discovery in Europe, it has been reported from a number of localities in Great Britain, but always on potato.

The recorded history of this species in the United States is interesting and begins with the collection of specimens on peas at San Jose, California, in 1912[19] by Edith M. Patch, who later received specimens found on Easter lily under glass from Canada in 1916, and collected it from a large number of host plants at Orono, Maine, in 1922–1925. After a thorough study of the species in Maine, Patch (1928) published a bulletin on the biology and host plants of the insect. Her list of all known food plants includes 72 species and 31 families. The foxglove, *Digitalis purpurea,* on which the aphid deposits the overwintering eggs, is considered to be the primary host in Maine; and the numerous other plants, upon which it feeds during the summer, are indicated as secondary hosts.

This aphid was later discovered in Colorado, and the writer has specimens collected on *Helichrysum* at Fort Collins by C. P. Gillette, September 3, 1925, and on potato at the same place by M. A. Palmer, April 4, 1930. Gillette and Palmer (1931–1934, vol. 27, p. 206) have also since found it feeding on the leaves of cineraria, gladiolus, *Helichrysum, Leonotis Leonurus,* lettuce, potato, and tomato at Fort Collins.

P. S. Bartholomew collected what appears to be this same aphid on the leaves of aucuba at Stanford University, California, April 12, 1930, which he described as *Macrosiphum aucubae* (Bartholomew, 1932).

Since then the writer has collected the same species in large numbers on the undersides of the leaves of *Aucuba japonica* on the campus of the University of California at Berkeley and at Stanford University.

The foxglove aphid is a fairly large species measuring from 2.0 to 2.5 mm in length. The apterous forms are robust, shining, pale whitish, yellowish green, or bright green, immaculate, except that in some individuals there are two darker-green patches, one at the base of each cornicle. The extreme apexes of antennal segments III to V are black, as is also most of segment VI, the apexes of the femora and tibiae, all of the tarsi, and the extreme apex of the cornicles.

The winged forms vary from yellowish to green and are variously marked with black as indicated in figure 9, *A*. The broken transverse bands on the dorsum of the abdomen and the black-tipped cornicles are characteristic. The most conspicuous anatomical character is the short

[19] The writer collected and mounted specimens from *Livistona chinensis* at Ventura, California, in 1910, but did not determine the species until recently.

imbricated area at the tips of the rather long, cylindrical, and somewhat tapering cornicles, which have conspicuous flanged openings. The lateral pigmented areas on the abdomen reveal groups of circular glandlike bodies which appear to be normal in the winged forms and may be of value in recognizing the species.

The colonies are sometimes very large. The individuals have a clever

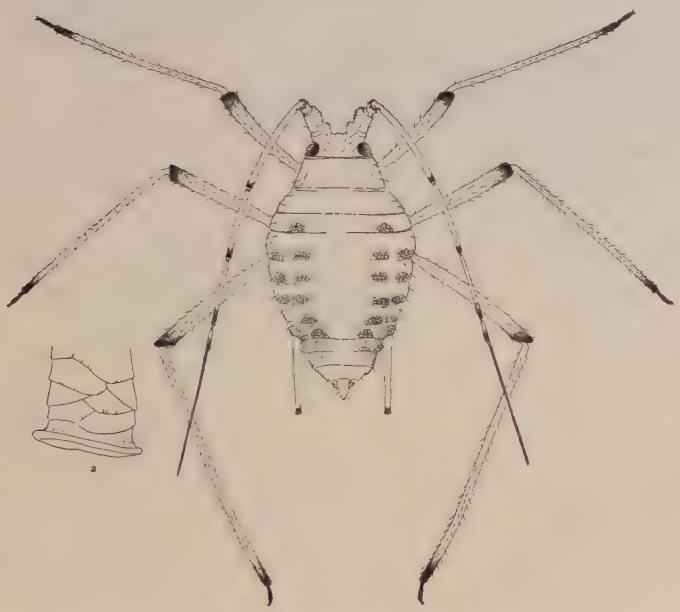

Fig. 10.—The foxglove aphid, *Myzus convolvuli* (Kaltenbach), adult apterous female: *a*, tip of cornicle. Other details are shown in figure 9.

way of standing head down, exuding a drop of honeydew, and then kicking it off with the hind legs, an operation not previously observed by the writer.

For a complete list of food plants, Patch (1928, p. 54–57) should be consulted. The list is too long to be included here. The most important hosts listed by her are: amaranthus, *Ambrosia,* apple, buttercup, calla lily, celery, chickweed, chrysanthemum, cinquefoil, clover, columbine, cudweed, dock, Easter lily, evening primrose, foxglove, gladiolus, goldenrod, groundsel, hawthorn, Jerusalem cherry, lamb's-quarters (*Chenopodium album*), mullein, orange hawkweed, pansy, pea, plantain, potato, purslane, shepherd's-purse, sow thistle, strawberry, tansy, verbena, and

violet. In California the species has become widely distributed, especially along the northern coast, and has been collected on the following plants:

Aucuba—Stanford University, by Bartholomew, 1930, Essig, 1935; Berkeley, by Essig, 1935, 1936
Bush monkey flower, *Diplacus aurantiacus*—Niles, by Essig, 1935
Carum—Berkeley, by C. F. Roesling, 1923
Celery—Berkeley in greenhouse, by Freitag, 1935, very small specimens collected at Venice
Cestrum—Berkeley, by Essig, 1935, 1936, and W. D. Riley, 1935, 1936
Columbine—Berkeley, by C. F. Roesling, 1923
Euphorbia Lathyrus—Berkeley, by Essig, 1936
Iris—Berkeley, by Elwyn Daybell, 1936
Latania—Ventura, by Essig, 1910
Milkweed—Berkeley, by C. F. Roesling, 1923
Pentstemon—Berkeley, by Essig, 1929
Stachys bullata—Pepperwood, by Essig, 1936
Vinca major—Berkeley, by Essig, 1936; Point Reyes Light House, by Essig, 1936

The writer took a winged specimen on the wing at Fort Seward, 1936. A single-winged specimen was also collected on *Lonicera involucrata* at Everett, Washington, July 17, 1935. It may have been just resting on that plant.

From the above records, it will be seen that the foxglove aphid has a wide distribution in this state and bids fair to become an insect of considerable economic importance.

On aucuba in Berkeley the aphid was parasitized to the extent of about 2 per cent by *Aphelinus jucundus* (Brullé). The parasitized individuals retained their normal size and shape, but became shining, jet black.

THE GREEN PEACH APHID[20]

Myzus persicae (Sulzer)
(*Aphis persicae* Sulzer)
[*Rhopalosiphum persicae* (Sulzer)]

The green peach aphid, *Myzus persicae* (Sulzer) (fig. 11), appears to be the most important aphid known as an agent in the dissemination of plant diseases and bids fair to become the insect most injurious to agricultural crops in many parts of the world. It enters extensively into all economic entomological literature and is responsible for distributing more plant viruses over wide areas than any other insect so far recorded.

Fortunately, this aphid is sufficiently distinct anatomically to make its identity fairly certain and easy, so that it has not generally been confused with a lot of other species, as have so many less characteristic aphids. It is of ordinary size, and yellow, green, or pinkish in color, all

[20] This insect has also been called the spinach aphid.

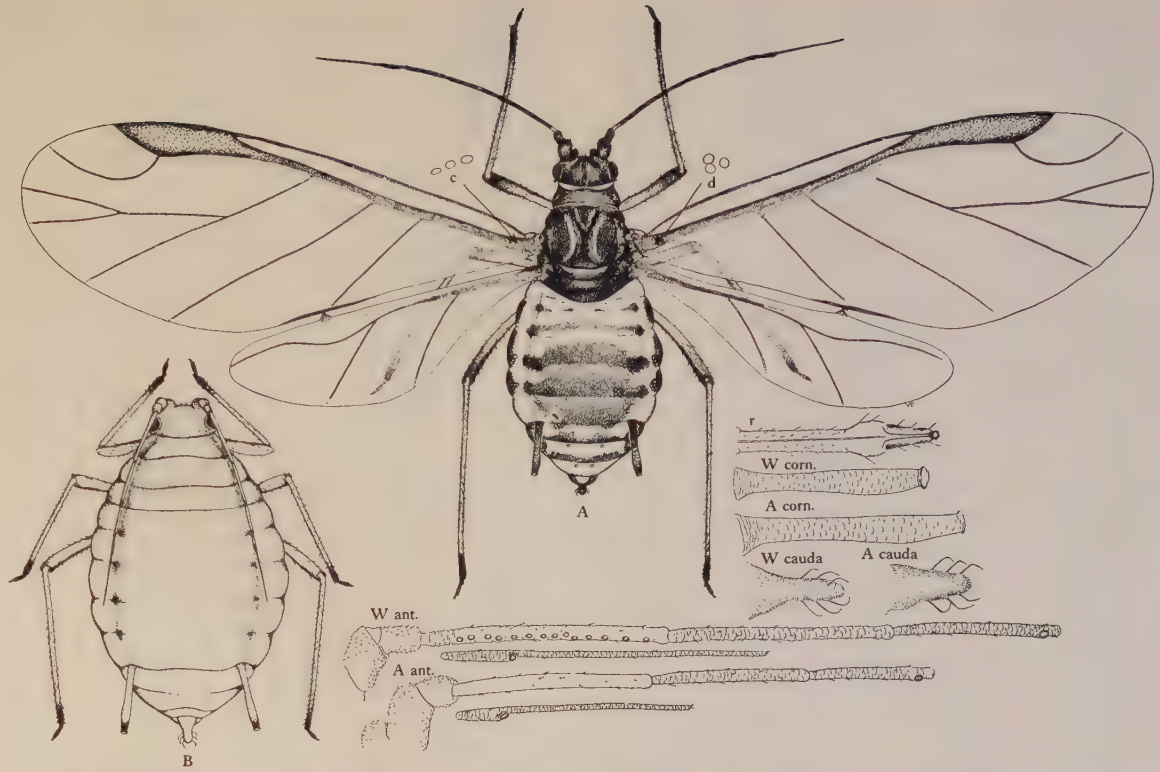

Fig. 11.—The green peach aphid, *Myzus persicae* (Sulzer). *A*, Adult winged female: *c* and *d*, fenestras on fore wings; *r*, rostrum; *W ant.*, antenna; *W corn.*, cornicle; *W cauda*, cauda. *B*, Adult apterous female: *A ant.*, antenna; *A cauda*, cauda. All greatly enlarged.

of these forms often occurring in the same colony. The wingless forms are without markings on the body proper. In the winged forms, the head, appendages, much of the thorax, and a conspicuous dorsal abdominal blotch and small lateral patches, are dusky or black. The third antennal segment of the winged form has a row of circular sensoria; and the cornicles are somewhat swollen, as shown in figure 11.

The life history of this aphid in California appears very simple. So far neither eggs nor true sexual males and females have been noted. The apterous and winged migrant viviparous females abound throughout the entire year over much of the state, and even in midwinter all forms and stages in development may be observed on many of its normal hosts. During the year eight or ten broods appear, which give rise to great numbers of individuals.

From the vast array of literature dealing with this insect, one could list hundreds of host plants and numerous, extensive, and widely separated habitats. In this paper only the more important hosts[21] are included for California and the western states, where the species is commonly and abundantly distributed. These hosts are: abutilon, amaranthus, *Amsinckia,* apple, asparagus, bean, beet, cabbage, calla, cantaloupe, carnation, catalpa, celery, *Chenopodium,* chrysanthemum, citrus (grapefruit, lemon, orange, etc.), clover, corn, cotton, cucumber, dahlia, dock, eggplant, English ivy, foxglove, fuchsia, lettuce, grape, lilies, malva, marigold, milkweed, muskmelon, mustard, nasturtium, nettle, onion, oxalis, parsley, peach, pear, pepper, plum, potato, prickly lettuce, prune, pumpkin, puncture vine, radish, rape, *Sanicula,* shepherd's-purse, snapdragon, sow thistle, spinach, squash, thistle, tobacco, tomato, tulip, turnip, *Vinca,* watercress, watermelon, wheat. During the winter and early spring it is often a most serious pest of spinach.

The green peach aphid may occur in few numbers scattered over the host as is the case during much of the season on many crops, or it may congregate in sufficient numbers to destroy the leaves and tender shoots completely. On spinach, lettuce, and similar succulent plants it may become exceedingly abundant and destructive. During the winter and especially in the early spring, when it may be numerous, it is commonly destroyed in great numbers by fungus diseases. During spring, summer, and autumn, insect predators and parasites thin out its ranks, but hardly reduce its numbers to the extent of affording control.

[21] Important lists of hosts of *Myzus persicae* (Sulzer) are as follows: Essig (1911, p. 600; 1917, p. 331–32; 1924, p. 253); J. Davidson (1925, p. 60); Hall (1926, p. 41–42); Mimeur (1934, p. 39); Swain (1919, p. 85); Wilson and Vickery (1918, p. 125–26); Theobald (1926–1929), vol. 1, p. 322–24); Smith (1937, p. 538–42; 1934, p. 109. Also see index.).

This aphid is one of the most widely distributed species known and occurs over much of the entire world. It undoubtedly inhabits many areas not reported as yet, but it has actually been observed in the following countries:

Africa: Egypt, Morocco, Nyasaland, Rhodesia, South Africa, Tanganyika.

Asia: Ceylon, China, India, Japan, Palestine, Transcaucasia.

Europe: Czechslovakia, Denmark, France, Germany, Great Britain, Holland, Italy, Jugoslavia, Norway, U. S. S. R., Switzerland.

North America: Bermuda, Canada, Guatemala, United States, West Indies (Jamaica and Puerto Rico).

South America: Argentina, Uruguay.

Oceania and the Pacific: Australia, East Indies (Java and Sumatra), New Zealand.

In the United States this aphid appears to have been reported from every state.

In California its distribution is confined chiefly to the cultivated areas, which indicates that it may have been introduced, although this is by no means certain. There are definite records from a great many localities throughout the entire state. Severin and Freitag collected it in the celery fields at Milpitas, December 19, 1935, and have reared it on celery in the greenhouse at Berkeley since that time.

THE HONEYSUCKLE APHID

Rhopalosiphum melliferum (Hottes)
(*Aphis xylostei* Schrank)
(*Rhopalosiphum xylostei* Koch)
(*Siphocoryne conii* Davidson)
[*Hyadaphis xylostei* (Schrank)]
(*Hyadaphis mellifera* Hottes)

The honeysuckle aphid, *Rhopalosiphum melliferum* (Hottes) (fig. 12), would certainly occupy a more prominent place in entomological literature if it had not so often been confused with the parsnip aphid, *Cavariella pastinacae* (Linn.)[22] and other related species. It was originally described as *Aphis xylostei* in Europe by Schrank as early as 1801 (Schrank, 1801, p. 107–8). For over a hundred years it has been shuffled into the various genera: *Aphis, Siphocoryne, Hyadaphis,* and *Rhopalosiphum,* without a permanent resting place in any of them.

In California the species first came to notice in 1909 when it was collected on the flower stalks and leaves of poison hemlock in the vicinity of Stanford University by W. M. Davidson (1909, p. 304), who described it as a new species, *Siphocoryne conii.* Later recognizing it as the European species named by Schrank, he relegated it as a synonym of *Siphocoryne xylostei* in 1914 (W. M. Davidson, 1914, p. 134), which he had

[22] Gillette (1911, p. 322–23) has fully discussed it as *Rhopalosiphum pastinacae* (Linn.).

already found curling the leaves of honeysuckle at Palo Alto some four years previously (Davidson, 1910, p. 377). In studying the species more recently, F. C. Hottes discovered that the name *Aphis xylostei* of Schrank had been preoccupied by *Aphis*[23] *xylostei* of De Geer, and he

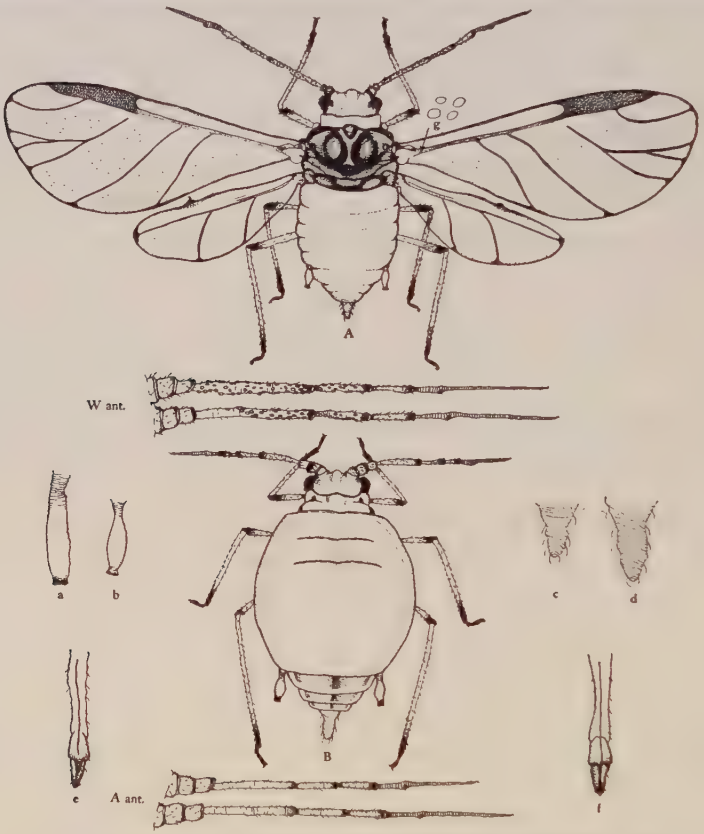

Fig. 12.—The honeysuckle aphid, *Rhopalosiphum melliferum* (Hottes). *A*, Adult winged female: *W ant.*, antennae; *b*, corniele; *c*, cauda; *e*, rostrum; *g*, fenestras. *B*, *Adult* apterous female: *A ant.*, antennae; *a*, corniele; *d*, cauda; *f*, rostrum. All greatly enlarged.

therefore renamed it *Hyadaphis mellifera* (Hottes, 1930, p. 184), which in 1931 was redefined as *Rhopalosiphum melliferum* (Hottes) by Hottes and Frison (1931, p. 238), by which name it is now known.

The species is subject to considerable variation in size. All specimens received from east of the Rocky Mountains taken on both the primary and secondary hosts appear to be very much smaller than the specimens received from Colorado and those collected in California. Living forms

[23] Now *Prociphilus xylostei* (De Geer).

reared on celery in the University greenhouse by Severin and Freitag present a most unusual spectacle. They are about one-fourth the size of normal individuals occurring in nature and appear like tiny replicas of the outdoor forms. That a species might be so altered by a change in environment and possibly also food scarcely seemed possible, and the writer would have been inclined to treat it as a distinct species, if other aphidologists, who examined mounted specimens, had not pronounced these small individuals to be *Rhopalosiphum melliferum*. Specimens collected on poison hemlock appear to reach the maximum development in size, the winged forms attaining a length of 2.0 mm, and the apterous forms 2.5 mm. The average length is approximately 1.5 mm to 2.0 mm, respectively.

The color also is variable. Those occurring on honeysuckle in California are striking in color, being uniform pale green covered with a fine whitish pulverulence as if frosted, and with conspicuous black head, antennae, thorax (in winged forms), legs, cornicles, anal plate, and genital plate, as indicated in figure 12. Davidson (1909, vol. 2, p. 304) refers to the color as bright green and Gillette and Palmer (1931–1934, vol. 25, p. 484) describe Colorado forms as "pale yellowish brown in alatae [winged forms], pale yellowish in apterae; all appendages dusky." Forms infesting poison hemlock in California are very dark olive-green and appear almost black as they occur in compact colonies in the flower umbels. Under greenhouse conditions, the general color is pale yellowish green with the various appendages faintly dusky.

Aside from the striking color combinations, the honeysuckle aphid may also be distinguished by the large numbers of secondary sensoria on antennal segments III and IV of the alates and by the peculiar, smooth cornicles, which are nearly straight along the outer margins and distinctly swollen along the inner. In some individuals the cornicles are noticeably recurved.

The species usually occurs in dense colonies. On the honeysuckle and snowberry, they infest chiefly the tips of the new growth and cause a curling of the leaves; on the poison hemlock, they are most conspicuous in the flower heads or umbels; while on celery, parsley, parsnip, and other plants, they occur on the undersides of the leaves. Since wild honeysuckle and umbelliferous plants occur abundantly in this state, the aphid is also probably widely distributed.

The distribution of this insect is very imperfectly known. Hottes and Frison (1931, p. 238) refer to it as a cosmopolitan species. In Europe it has been reported from Belgium, France, Germany, and Great Britain. In the United States reports have been noted or specimens received from

California, Colorado, Illinois, Indiana, Missouri, New York, and South Carolina. It no doubt also occurs in other states.

The primary or winter hosts consist of many species and varieties of honeysuckle (*Lonicera* spp.) and snowberry (*Symphoricarpos* spp.); and the secondary or summer hosts are chiefly umbelliferous plants. The host records for all regions include, in addition to the above: *Berula erecta, Carex* spp., celery, *Cicuta, Conioselinum chinense, Cryptotaenia canadensis, Heracleum lanatum,* parsley, parsnip, and poison hemlock.

The known host and locality records for California possessed by the writer are:

Celery—Berkeley (in greenhouse), by Severin and Freitag, 1935, 1936.

Honeysuckle (cultivated and native)—Claremont, by Essig, 1909; Walnut Creek, by W. M. Davidson, 1913; Berkeley, by Essig, 1915, 1916, 1935; Garberville, by Essig, 1935; Fort Seward, by Essig, 1935; Inverness, by Essig, 1936; Arcadia, by Michelbacher, 1926.

Poison hemlock—Stanford University, by W. M. Davidson, 1909; San Jose, by W. M. Davidson, 1911; Berkeley, by Essig, 1935; Alvarado, by Essig, 1935.

Snowberry—Niles Canyon and Livermore, by Essig, 1935.

OTHER APHIDS ATTACKING CELERY

The African Celery Aphid.—The African celery aphid, *Aphis apiifolia* (Theobald) (*Anuraphis*), has been taken on celery in Egypt (Theobald, 1922*b*, p. 59), on celery in Morocco (Mimeur, 1934, p. 23), and on celery and sweet fennel (*Foeniculum vulgare*) in Egypt (Hall, 1926, p. 8). It has never been reported from this country.

The Dock Aphid.—The dock aphid, *Aphis rumicis* Linn., a very common and general feeder, was collected on celery at Milpitas, California, by Freitag on December 19, 1935. It has not been reared on celery.

The Tulip Aphid.—The tulip aphid, *Aphis tulipae* (B.d.Fonsc.), is a common species in California and is especially abundant on the rhizomes in storage, at the bases of growing plants, and under the leaf sheaths of all kinds of garden irises. It also occurs on tulip, gladiolus, scilla, crocus, chinodoxa, and on the roots of carrot and parsley (Theobald, 1926–1929, vol. 2, p. 241). Ogilvie (1927) reports it as feeding at the bases of carrot and celery in Bermuda.

The Green Apple Aphid.—The green apple aphid, *Aphis pomi* De Geer, has been reported on celery in Florida by Cole (1926). Although abundant in California on many hosts, it has not been taken on celery.

Hall's Celery Aphid.—Hall's celery aphid, *Hyadaphis apii* Hall, has been reported on celery in Egypt by Hall (1926, p. 20) and on the same host in Morocco by Mimeur (1934, p. 18–19).

Theobald's Celery Aphid.—Theobald's celery aphid, *Cavariella theo-*

baldi (Gillette), has been reported as taken from celery in Colorado by Gillette and Palmer (1932, p. 468–69).

The Wild Lettuce Aphid.—The wild lettuce aphid, *Myzus lactucae* (Schrank), has been listed from celery in Illinois by Hottes and Frison (1931, p. 339).

SUMMARY

In California aphids are playing an important rôle in the transmission of virus diseases of celery and are thereby causing considerable financial loss to the producers of that crop. To date eleven species on celery in this state may be considered as potential pests. They are: (1) the celery leaf aphid, *Aphis apigraveolens* Essig n. sp.; (2) the celery aphid, *Aphis apii* Theobald; (3) the rusty-banded aphid, *Aphis ferruginea-striata* Essig n. sp.; (4) the cotton or melon aphid, *Aphis gossypii* Glover; (5) the cow parsnip aphid, *Aphis heraclella* Davis; (6) the erigeron root aphid, *Aphis middletonii* Thomas; (7) the yellow willow aphid, *Cavariella capreae* (Fab.); (8) the lily aphid, *Myzus circumflexus* (Buckt.); (9) the foxglove aphid, *Myzus convolvuli* (Kaltenbach); (10) the green peach aphid, *Myzus persicae* (Sulzer); and (11) the honeysuckle aphid, *Rhopalosiphum melliferum* (Hottes). The dock aphid, *Aphis rumicis* Linn., was also taken once on celery in California, but has not been reared on that plant. The majority of these are undoubtedly introduced species.

Nearly all of them have a number of hosts. The cotton or melon aphid, the lily aphid, the green peach aphid, and the foxglove aphid have many and varied hosts.

All of these species appear to reproduce parthenogenetically continuously during the entire year, although there is a noticeable reduction of individuals during the winter months.

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WESTERN CELERY MOSAIC

HENRY H. P. SEVERIN AND JULIUS H. FREITAG

CONTENTS

WESTERN CELERY MOSAIC[1]

HENRY H. P. SEVERIN[2] AND JULIUS H. FREITAG[3]

WESTERN CELERY MOSAIC has increased in the celery-growing districts in Los Angeles, Orange, San Mateo, Santa Clara, Alameda, Yolo, and Sacramento counties and is causing serious losses to the growers. The destructiveness of western celery mosaic was evidenced by a reduction in yield in the Venice district: Milbrath (*17*)[4] reported that in 1932 a total of 2,737 cars of celery went from that district; in 1933 there were about 982 cars, and the estimate for 1934 is less than 500 from approximately the same acreage. Brock (*1*) estimated that in 1934 celery mosaic in the Venice district reduced the production of celery to about 16 per cent of normal car loadings. The decline in yields during 1930–1934 in two celery districts in Los Angeles County is shown in table 1.

TABLE 1

YIELDS OF CELERY IN THE VENICE AND CULVER DISTRICTS, LOS ANGELES COUNTY

Year	Acreage	Yield per acre, in half crates	Production, in half crates
1930	700	1,026	718,200
1931	1,100	740	814,000
1932	1,500	661	991,500
1933	1,300	555	721,500
1934	900	311	279,900
1935*	200	800	160,000
1936†	950	926	879,700
1937†	950	847	804,650

Sources of data:
* 1930-1931: from Milbrath (*18*, *19*).
† 1932-1937: Milbrath, D. G., and Harold J. Ryan. A method of control of western celery mosaic. California State Dept. Agr. Mo. Bul. 27 (3): 290-95. 1938.

In 1933 the f.o.b. value of the celery crop in Los Angeles County was $1,965,455. This value was exceeded by only two other crops—citrus and walnuts. In 1934, the f.o.b. value of the celery crop was $838,490; the celery crop was fifth in importance.[5]

Celery infected with western celery mosaic when shipped to the middle western and eastern markets becomes soft in transit according to growers.

[1] Received for publication November 15, 1937.

[2] Associate Entomologist in the Experiment Station.

[3] Junior Entomologist in the Experiment Station.

[4] Italic figures in parentheses refer to "Literature Cited" at the end of this paper.

[5] Milbrath, D. G., letter to senior author dated September 16, 1935.

This results in a total loss to the grower, who, in addition, is required to pay the freight. In the local markets diseased celery also becomes soft when kept on the vegetable stands for a few days.

An investigation was undertaken on the host range, properties of the virus, and the relative importance of different species of aphid vectors of the virus of western celery mosaic. Other aspects of aphid transmission of the virus of western celery mosaic discussed in this paper include a comparison of the transmission of the virus by different species of aphids with mechanical inoculation, a comparison of the transmission of the virus by single winged and wingless mature aphids, the retention of the virus by aphids, and loss and recovery of the infectivity by aphids on inoculated plants.

CELERY VIRUS DISEASES

Six virus diseases of celery (*Apium graveolens* var. *dulce*) occur under natural conditions in California as follows: western celery mosaic, celery calico, celery yellow spot, celery crinkle-leaf, celery yellows (the virus is identical with California aster yellows), and spotted wilt. Celery has been experimentally infected with the virus of poison-hemlock ringspot and sugar-beet curly top, but these diseases have not been found in celery fields up to the present time. Some of the virus diseases of celery discussed in the following paragraphs have been shown to be caused by the cucumber-mosaic virus or a strain of this virus. A brief review of the occurrence of celery-mosaic diseases in the United States and Europe is given.

Western Celery Mosaic.—Celery mosaic from California differs from southern celery mosaic in symptoms and host ranges (to be discussed later), and the viruses differ in properties. The common name "western celery mosaic" was therefore suggested (*32*) for the California disease to distinguish it from southern celery mosaic. The disease is common in the Fog Belt of California and also occurs in the hot interior regions, such as the Sacramento Valley.

Celery Calico.—The common name used by the present writers (*32*) for another celery mosaic disease is "calico." Considerable variation occurs in the development of the early symptoms of celery calico. The symptom which sometimes develops first in the greenhouse is a clearing of the veins with a slight yellowing along them (plate 1, *A*), accompanied by a puckering and downward cupping of the younger leaves. Frequently no vein clearing occurs, but a faint yellowing develops near the basal region of the leaflets (plate 1, *B*), or pale-yellow bands appear across the leaflets (plate 1, *C*), and later change to amber-yellow or pale orange. A reliable symptom in a later stage of the disease is green islands

in the lemon-yellow areas (plate 1, *D*) of the outer leaves. Sometimes the green areas are surrounded by chlorotic rings, resembling ringspot (plate 1, *E*). In the more advanced stages of the disease, the leaflets may show green and yellow zigzag bands and many small green islands (plate 1, *F*). Celery calico has been found in all of the large celery districts of California.

Celery Crinkle-Leaf.—Another virus disease of celery has been named "crinkle-leaf mosaic." The first symptom of the disease on the youngest

Fig. 1.—Petioles from celery (*Apium graveolens* var. *dulce*) naturally infected with celery yellow spot: left, petiole from a healthy celery plant; right, three petioles showing white spots (Milpitas, October 17, 1935).

leaves is a clearing of the veinlets, sometimes restricted to the basal portion of the leaflets (plate 2, *C*). The most conspicuous symptom which develops later is crinkle leaflets with green islands or blisterlike elevations (plate 2, *D*). Young infected plants are stunted, and in the later stages of the disease, the leaves turn yellow and frequently the plant dies. This disease has been found in the celery districts of the Santa Clara Valley.

Celery Yellow Spot.—The name "yellow spot" is proposed for a virus disease of celery that is characterized by small irregular chlorotic areas on the leaves (plate 2, *A*) and yellow stripes or bands along the veins (plate 2, *B*). The petioles frequently show white spots (fig. 1), and when the epidermis is removed brown specks may be seen along the veins (plate 3, *E*). This disease occurs in the Santa Clara, Salinas, and Sacramento valleys.

Celery Yellows.—The virus of celery yellows has been demonstrated to be identical with that of California aster yellows. Both diseases have been discussed in a previous paper (*28*).

Spotted Wilt.—The following description of the symptoms of spotted wilt on celery has been contributed by M. W. Gardner:

Spotted wilt, a disease caused by a thrips-transmitted virus attacking a wide range of truck crops and ornamentals especially in the coastal districts, is very destructive in its effects on celery. Infected celery plants show numerous small yellow spots on

Fig. 2.—The spotted-wilt virus produces numerous yellow spots on the celery leaves; later these spots become brown and dead at the center (San Pablo, September 18, 1934, courtesy of M. W. Gardner).

the blades of the older leaves (fig. 2). These spots soon become brown and dead at the center. More serious, however, are large pockets of brown dead tissue, often entirely internal, which occur in the stalks of the older leaves (fig. 3). These leaf stalk lesions may become visible as sunken brown patches and eventually may kill the entire leaf. Frequently the dead areas are invaded by rot-producing organisms.

Plants infected early are greatly stunted and never become marketable. Plants infected late must be carefully examined and heavily pruned to remove all of the stalks that show dead spots, which are, needless to say, extremely objectionable to the consumer. Often the internal dead patches are difficult to detect without slicing the stalk with a knife.

Gardner, Tompkins, and Whipple (*11*) report that spotted wilt is most prevalent and severe in the cooler coastal districts of California, par-

ticularly where truck crops or ornamentals are grown to some extent throughout the year.

Sugar-Beet Curly Top.—The varieties Golden Self-blanching, Giant Pascal, and White Plume celery have been experimentally infected with the virus of sugar-beet curly top (*28*), but celery has not been found naturally infected up to the present time.

Poison-Hemlock Ringspot.—Celery has been experimentally infected with poison-hemlock ringspot. The symptoms on celery are character-

Fig. 3.—Spotted wilt in celery is characterized by large pockets of dead tissue in the leaf stalks, sometimes conspicuous like these, sometimes entirely internal and difficult to detect without slicing the stalks with a knife (San Pablo, December 4, 1935, courtesy of M. W. Gardner).

ized by small chlorotic rings enclosing green spots (plate 2, *E*) or by a series of chlorotic dots and dashes encircling irregular green areas. The chlorotic ring may be surrounded by a green line and both are sometimes embedded in a pale-yellow halo. Sometimes large, green, irregular areas are surrounded by alternating yellow and green lines (plate 2, *F*).

Southern Celery Mosaic (*Celery Virus 1*).—Foster and Webber (*9*) were first to describe celery mosaic in Florida. Southern celery mosaic has been reported by Doolittle and Wellman (*5*) from Florida and by Wellman (*38*) from Cuba. Plants having apparently identical symptoms have been found by these scientists in California, Wisconsin, Ohio,

and New York (*5*). Doolittle and Wellman (*5*) reported the transmission of the southern-celery-mosaic virus to cucumbers by the cotton or melon aphid (*Aphis gossypii* Glover) and by mechanical inoculation. Wellman (*36, 40*) came to the conclusion from his host-range studies and experimental results on the properties of the virus, that the virus of southern celery mosaic is new and distinct from that of cucumber mosaic.

Wellman published a number of other papers on southern celery mosaic. He reported (*35*) the control of southern celery mosaic by the eradication of the monocotyledonous host commonly known as "day flower" or "dew flower" (*Commelina longicaulis* = *C. nudiflora*), one of the main reservoirs of the virus. In another contribution (*37*), he found that the southern-celery-mosaic virus when inoculated mechanically or by the cotton or melon aphid and the corn-leaf aphid (*A. maidis* Fitch) in two species of banana plants produced a disease markedly similar to bunchy top. He also reported (*38*) the susceptibility of other monocotyledonous host plants to the virus. He observed (*39*) that field dissemination of the virus depended largely on infective aphids walking from plant to plant or flying from one part of the field to another, and correlated (*38, 54*) east winds with the dispersal of winged aphids. He reported a minor spread of the virus through mechanical means, and stated that the initial appearance of the disease usually occurs on the edge of the field from diseased weeds or economic plants.

Price (*23*) reported that there is a specific immune reaction between southern-celery-mosaic virus and cucumber-mosaic virus, showing that they are closely related and that they should be classified as strains of the same virus. He found that plants which were previously reported to be immune to southern celery mosaic and cucumber mosaic are, in fact, susceptible. These findings suggest that the host range of cucumber mosaic and celery mosaic may eventually be found to be identical. The virus causing southern celery mosaic should be designated as a strain of cucumber mosaic.

Cucumber Mosaic (*Cucumber Virus 1*).—A celery mosaic which causes a pronounced filiformity of the leaflets has been described by Poole (*22*) in New Jersey, Harvey (*13*) in Minnesota, and Elmer (*6*) in Iowa. Wellman (*36*) "was convinced that Poole, Harvey, and Elmer were working with common cucumber mosaic (cucumber virus 1 Doolittle [*3*]) on celery." Johnson and Grant (*15*) infected celery with cucumber mosaic in their studies on the properties of plant viruses from different host species.

Doolittle (*3*) reported the transmission of the cucumber-mosaic virus by the cotton or melon aphid (*Aphis gossypii*) and by mechanical inocu-

lation to celery. Wellman (*36*) states that the leaves on celery infected with cucumber mosaic, after about a month, showed filiformities and raised blisterlike areas following a mild mottling.

Distribution of Celery Mosaic.—Numerous other references of the occurrence of celery mosaic in the United States have appeared in the literature, especially in the *Plant Disease Reporter*, but in most cases the identification of the virus cannot be determined from these limited reports. "Celery mosaic" has been recorded from the following states:

California (*5, 8, 45, 48, 49, 56, 58, 59*) (western celery mosaic [*16, 21*], celery calico, and celery yellow spot [*16*] have been specifically recorded)
Connecticut (*51, 56, 58*)
Florida (*44, 47, 49, 51, 52, 53, 55*), Chicago market celery (*57, 58*)
Indiana (*10, 42, 43*)
Iowa (*47, 48, 58*)
Massachusetts (*41*)
Michigan (*58*)
Minnesota (*43*)
New Jersey (*43, 47*)
New York, market celery (*5, 45, 47, 48, 55, 56, 58*)
Ohio (*5, 46, 48*)
Utah (*50*)
Wisconsin (*5*)

Gigante (*12*) described the symptoms of a celery mosaic in Italy. Light-green or yellowish chlorotic areas and dark-green patches occurred on the leaves, which were wrinkled, with irregular midribs, greatly swollen underneath. Light—later dark-brown—elongated areas were present on the stalks, which curved over, forming an arc. The virus was transmitted by juice inoculations and by the aphid *Cavariella pastinaceae* Linn. from diseased to healthy celery and also to pumpkin.

MATERIALS AND METHODS

Source of Virus.—The source of the western-celery-mosaic virus used in the work on host range and property studies was naturally infected celery plants obtained in the Santa Clara Valley. The virus was retained by repeated mechanical inoculation and aphid transmission to celery.

Celery Extract.—In the preparation of juice from the leaves from western-celery-mosaic plants, the leaves were washed in distilled water and either ground to a pulp in a sterilized food chopper or in a mortar. The pulp was then placed in two layers of cheesecloth and the juice pressed out into a sterilized beaker or pan by hand.

Centrifugation.—In the work on filtration, the extracted juice was centrifuged for 1 hour at a speed of 3,500 revolutions per minute.

Mechanical Inoculation.—The method of mechanical inoculation used is that described by Rawlins and Tompkins (*24*). Shortly after inoculation, the carborundum and inoculum was washed from the leaves with water. The virus extract was usually inoculated in 5 healthy celery plants with each preparation.

Collecting and Rearing Aphids.—Various methods were used in determining the presence of aphids on celery. High populations of aphids were rarely found on celery under natural conditions during the summer. When the population of aphids was low on diseased celery shipped by scientists and growers, celery leaves were removed from the plants and shaken over black sateen; the aphids which dropped from the foliage were then transferred with a moistened camel's-hair brush to potted healthy celery plants enclosed in cages. The method finally adopted to secure both foliage and root-feeding aphids was to pot diseased celery plants obtained from the field, enclose them in cages, and allow the aphids to multiply.

A number of requests have been received from plant pathologists for a description of the methods used in rearing aphids in the greenhouse. Foliage-feeding aphids reared on celery grown in the greenhouse will die if transferred to celery with hardened leaves grown out of doors during late autumn and winter. Celery grown out of doors when kept in cages in the greenhouse will develop tender inner leaves on which the aphids can be reared. Low mortality of aphids occurred on celery grown in the greenhouse.

Mixed populations of different species of aphids or parasitized or fungus-diseased aphids were frequently collected in celery fields. Each species of aphid in a mixed population was removed with a camel's-hair brush under a binocular microscope. Young aphids were selected in an attempt to eliminate parasitized or fungus-diseased aphids. When a small braconid parasite, *Lysiphlebus testaceipes* (Cresson) emerged from the aphids, all aphids in the cage became parasitized. All parasites and parasitized or "mummied" aphids were removed from the cages. High humidity in the greenhouse and excessive soil moisture in the pots stimulate fungus diseases of the aphids. To eliminate high humidity and high temperatures in the greenhouse, the upper and lower vents were kept open day and night during the summer, which gave plenty of air circulation, and to lower the temperature, all glass of the greenhouse was whitewashed. The surface of the soil in the pots was covered with about an inch of dry coarse sand. Each pot was placed in a clay

saucer and the saucers were watered whenever they became dry. The cages used have been described and figured in a previous paper (*29*).

Aphids will usually die if placed on celery just after spraying with nicotine sulfate (Black Leaf 40) or Ortho Nursery Volck (or a combination of the two, or after fumigating with Nico-Fume tobacco-paper insecticide. Sprayed or fumigated plants can be used a few days after treatment, with the exception of plants sprayed with Ortho Nursery Volck, which must be thoroughly washed from the leaves with cotton swabs immersed in water.

In the greenhouse, control measures must be adopted against the Argentine ant (*Iridomyrmex humilis* Mayr), which enters the cages and carries away the aphids. Tree tanglefoot was applied to the legs below the tops of the tables on which rested the potted plants enclosed in cages.

One experience in which many colonies of aphids were lost may be worthy of mention. Creosote was applied to new floors in the greenhouse with the vents closed during the night; by the next morning most of the aphids had been killed by the fumes. The creosote, however, acted as an effective repellent for the Argentine ant for a long time.

Production of Noninfective Aphids.—In order to obtain noninfective aphids for experimental purposes, wingless mature aphids were transferred from western-celery-mosaic plants to healthy celery. The next day the offspring from the mature forms were transferred to a second healthy celery plant or to a plant immune to the disease.

Methods of Transferring Aphids.—Both noninfective and infective aphids were transferred, whenever a new food supply was necessary, by cutting off and placing the leaves with high populations of aphids on the inner or youngest leaves of another plant. If an accurate count of the number of aphids was desired, the aphids were transferred from plant to plant with a moistened camel's-hair brush. The mortality as the result of the transfers was low when the aphids were first induced to withdraw their mouth parts from the food plant by gently touching them on the abdomen with a camel's-hair brush.

SYMPTOMATOLOGY

The most striking symptoms of western celery mosaic on small plants as seen in the field are the yellowed foliage, stunting of the plant, shortening of the central younger petioles, and horizontal instead of upright position of the outer petioles, which gives the top of the plant a flattened appearance. An examination of the foliage of celery-mosaic plants in the Fog Belt shows speckling of green and yellow or mottling on the younger leaves; but in the hot interior regions such as the Sacramento Valley,

these symptoms are often absent during the summer. As the disease progresses, the older leaves sometimes show rusty or brown, necrotic, sunken areas on the upper surface of the leaves. The petioles sometimes show white streaks or spots.

The first symptom of western celery mosaic observed under a binocular microscope on white varieties of celery infected either by aphids or by mechanical inoculation is a clearing of the veins and veinlets and puckering of the youngest leaves (plate 3, *C, D*), but with the naked eye the veinlets appear white. The cleared veinlets occasionally appear within 4 days on small plants after inoculation, but on larger plants usually require from 1 to 2 weeks in the greenhouse and from 10 to 16 days or longer out of doors during the summer. The interspaces between the veinlets are green, but later some of the interspaces turn yellow, which causes a mottling (plate 4, *A, B, C*). The older leaves may show speckling and bands of green (plate 4, *D*) or most of the margin may be green (plate 4, *E*) or yellow (plate 4, *F*).

As the disease progresses, rust-colored necrotic specks which later turn brown may develop on the upper surface of the outer leaves (plate 5, *A*). Brown necrotic spotting developed in from 1 to 2 weeks after the cleared veinlets appeared when inoculated plants were kept out of doors during the summer, but this symptom rarely developed in the greenhouse. The brown specks enlarge to necrotic sunken areas and, as they become more abundant, frequently coalesce to form streaks or irregular patterns along the margins, which may spread over most of the leaflets (plate 5, *B*).

In the advanced stage of the disease, the leaflets are narrow, twisted, and cupped (fig. 4). The petioles sometimes show longitudinal white streaks (plate 3, *B*) alternating with green streaks, or more often the petioles show white spots (plate 3, *A*).

The symptoms of the disease on Utah celery, a green variety, are not as conspicuous in the field as on the white varieties. Frequently the youngest leaves are yellow with faint mottling, and often the leaflets are twisted and cupped. The outer leaves may show mottling.

A comparison of the symptoms of the disease on naturally and experimentally infected celery in early and late stages indicates that this disease is identical in all of the localities shown in table 13 (pp. 522–24).

Differentiating from Southern Celery Mosaic.—The early symptoms of southern celery mosaic on the leaves are similar to those of western celery mosaic. Wellman (*40*) describes the former as follows:

> The inoculation studies have shown that the first symptom of southern celery mosaic on young leaves is a faint vein-clearing pattern, which occurs under the most favorable greenhouse conditions in about 6 days, although it may take 10 to 40 days

for it to appear in the field. The vein-clearing pattern on leaves usually changes in about 10 days to a brilliant yellow mottling that, about a month later, is not so marked. Secondary systemic symptoms in older leaves result in yellowish oak-leaf patterns which in some cases take the form of continuous zigzag bands across the leaf lamina, and in other cases are markedly irregular and may break up into chlorotic blotches and spots.

Fig. 4.—Center, celery leaflets from a healthy plant; grouped around it are four celery leaflets from a plant naturally infected with western celery mosaic showing narrow, twisted or cupped leaflets (Gardena, July 1, 1935).

In the description of symptoms of southern celery mosaic, no mention is made of rust-colored or brown necrotic specks, streaks, or irregular patterns on the upper surface of the older leaves, which are characteristic of western celery mosaic after secondary systemic symptoms developed.

As the disease progresses, buff, almost salmon-colored, water-soaked spots and sunken streaks develop on the petioles of southern-celery-mosaic plants, and the vascular system of the petioles and leaf rachises is

often discolored or darkened throughout. The dark or streaked petioles later become brown, shriveled, and necrotic, and finally decay. These symptoms have never been observed on western-celery-mosaic plants, but rather the petioles sometimes show white streaks or spots. When a celery plant is infected with both western celery mosaic and spotted wilt, severe necrosis of the petioles occurs, but necrosis is caused by the virus of spotted wilt.

CAUSES OF LEAF ABNORMALITIES IN CELERY

Club-shaped Leaves.—Celery with malformed or club-shaped leaves (fig. 5), sometimes with shoots growing below the crown (fig. 6), have been found in celery districts where the leaves were cut back in the seed

Fig. 5.—Malformed or club-shaped celery leaves developed by cutting back the crown or by improper transplanting so that the root is curved up in the soil (Terminus, San Joaquin Valley, September 17, 1936).

bed. According to the opinion of celery growers, these abnormalities are caused by cutting back the crown or by improper transplanting so that the root is curved up in the soil. Sometimes these abnormal celery plants were infected with western celery mosaic (plate 6, *C*), as was demonstrated by juice inoculation and by transmission of the virus by the cotton or melon aphid (*Aphis gossypii*); but the malformed leaves were caused by cultural conditions.

Linear Leaflets.—Celery was sometimes found under natural conditions with narrow or linear leaflets (plate 6, *E*), resembling those caused by cucumber mosaic. Occasionally these abnormal celery plants were infected with western celery mosaic, but not with cucumber mosaic, as was

Fig. 6.—Celery plant showing abnormal leaves and with shoot growing below the crown caused by cutting back the crown (Terminus, San Joaquin Valley, September 17, 1936).

demonstrated by juice inoculation. On rare occasions healthy celery plants may develop narrow leaflets (plate 6, *F*). Celery experimentally infected with western celery mosaic sometimes develop abnormal leaflets; for example, a portion of one leaflet may be narrow (plate 6, *B*) or all leaflets may be narrow with the exception of the apical leaflet (plate 6, *A*). On one occasion a celery plant was found on which the leaflets

showed blisterlike pustules (plate 6, *D*) resembling those caused by cucumber mosaic on celery, but all attempts to transmit the virus to healthy celery and cucumber plants by juice inoculations were failures. Aphid transmission was not tested.

Curling of Leaflets.—Different species of noninfective aphids feeding on healthy celery plants produced abnormalities of the leaflets. Noninfective cotton or melon aphid, *Aphis gossypii,* feeding on the foliage of healthy celery plants produced curling of the leaflets (plate 7, *A*), which may be caused by the destruction of some leaf tissue to the phloem by the feeding punctures of large number of aphids.

Yellowing and Chlorosis.—Noninfective yellow willow aphids, *Cavariella capreae* (Fabr.), feeding on healthy celery plants, produced a pronounced yellowing along the cleared veins (plate 7, *B*) and a marked chlorosis of the leaflets, probably caused by the saliva of the aphids. Noninfective foxglove aphids, *Myzus convolvuli* (Kalt.), feeding on the leaflets of healthy celery plants, produced white spots (plate 7, *C*, *D*), the latter resembling the symptoms of yellow spot except in color. The curling of the leaflets may be caused by the punctures of the mouth parts and the white spots by the saliva of the aphids.

When celery plants showing curled leaflets, or yellowing along the cleared veins, or curled leaflets with white spots produced by the three species of aphids, were fumigated and all of the aphids were killed, the new leaves which developed were normal; this indicated that the toxic substance in the saliva affected only the leaves on which the aphids had fed. On the other hand, when the honeysuckle aphids (*Rhopalosiphum melliferum*), which transmit the virus of celery yellow spot, were killed by fumigation, the new leaves which developed showed the yellow spots; this indicates that the virus had spread to the youngest leaves.

HOST RANGE

Natural Infection.—The following economic plants have been found to be naturally infected with western celery mosaic up to the present time. The virus was recovered by inoculation of extracted juice from these host plants into healthy celery.

Celeriac (*Apium graveolens* var. *rapaceum*)

Carrot (*Daucus Carota* var. *sativa*), varieties Chantenay, Chantenay Red Cored, Danvers Half Long, Imperator, and Short Top

Experimental Infection.—The following plants—all economic—of the family Umbelliferae, are the only ones other than celery which have been infected thus far.

Large Smooth Prague celeriac (*Apium graveolens* var. *rapaceum*)
Dill (*Anethum graveolens*)
Curled chervil (*Anthriscus Cerefolium*)
Caraway (*Carum carvi*)
Coriander (*Coriandrum sativum*)
Carrot (*Daucus Carota* var. *sativa*); white varieties: Short White, White Mastodon, and White Belgian; yellow variety: Yellow Belgian; orange varieties: Chantenay, Chantenay Red Cored, Danvers Half Long, Early Scarlet Horn, French Forcing, Imperator, Long Orange, Nantes, and Oxheart, or Guerande
Single or Plain parsley (*Petroselinum hortense*)

Fig. 7.—Large Smooth Prague celeriac (*Apium graveolens* var. *rapaceum*); upper row, leaflets from a healthy plant; others from a plant infected with western celery mosaic by the rusty-banded aphid (*Aphis ferruginea-striata*), showing blotches which were deep green scattered in the chlorotic areas of the leaflets.

Recovery of Virus.—The virus was recovered from the experimentally infected host plants by inoculation of extracted juice or by previously noninfective rusty-banded aphids (*Aphis ferruginea-striata* Essig) into healthy celery. All inoculated economic plants and weeds which failed

to show symptoms of the disease were also tested for the recovery of the virus by both methods.

Symptoms.—The symptoms of western celery mosaic on different host plants are, briefly, as follows:

Large Smooth Prague celeriac: The first symptom of the disease observed under a binocular microscope is a clearing of the veins, accompanied later by chlorosis along the veins, followed by mottling. The

Fig. 8.—Longitudinal section of celeriac (*Apium graveolens* var. *rapaceum*) naturally infected with western celery mosaic, showing mottling of the leaves and shortened inner or central petioles (Alvarado, December 19, 1935).

mosaic pattern consists of deep-green blotches scattered in chlorotic areas of the leaflets (fig. 7). Naturally infected celeriac showed mottled leaves and shortened inner or central petioles (fig. 8).

Dill: A single plant was infected with western celery mosaic by the rusty-banded aphid, and the only symptom of the disease observed was chlorotic secondary shoots arising from the axil of the leaves.

Curled chervil: The first symptom of the disease is a yellowing along the veins, followed by chlorotic spotting of the inner or youngest leaves.

In the later stage of the disease, the outer leaves show brown spotting followed by necrosis (plate 5, *F*). The leaflets finally turn yellow and die.

Coriander: The earliest symptom of the disease was a clearing of the veinlets (plate 8) on the youngest leaves, followed later by a mottling of the older leaves (plate 8), which frequently became cupped outward. The stems were chlorotic, and infected plants were stunted.

Carrot: Plants infected with western celery mosaic by the rusty-banded aphid showed chlorotic areas on the youngest leaflets (plate 5, *C*) followed by mottling (plate 5, *D, E*).

Single or Plain parsley: Fifty plants were inoculated mechanically or by the rusty-banded aphid with the virus of western celery mosaic, but only 10 plants developed mild symptoms of the disease. A slight chlorosis appeared along the midrib and lateral veins and spread as blotches over the leaflets. Frequently only the leaflets of a few outer leaves showed these symptoms. No cleared veinlets were noted on the inner or youngest leaves.

INOCULATION EXPERIMENTS

Extracts from Diseased Carrots.—In a previous experiment, Severin and Freitag (*31*) reported that the curly-top virus could be transmitted more successfully to healthy beet seedlings by previously noninfective nymphs fed on diseased beet-root juice than by means of those fed on leaf juice. A somewhat similar experiment was performed with the extract from the leaves and roots of mosaic carrots inoculated with carborundum in healthy celery plants. The juice was expressed from the leaves and roots of 9 varieties of carrots naturally or experimentally infected with western celery mosaic. In each test the juice from each variety of carrot was expressed from the leaves and roots and inoculated into healthy celery plants.

The results obtained are shown in table 2. According to these data, the average percentage of infections was higher with diseased root juice, 76.0 and 79.0 per cent, from naturally and experimentally infected carrots respectively, as compared with 36.0 and 54.0 per cent with leaf juice. Table 2 shows that 6 of 10 preparations from the leaves and all 10 preparations from the roots of naturally infected carrots were infectious, and 18 of 20 preparations from the leaves and 19 of 20 preparations from the roots of experimentally infected carrots were infectious.

Extract from Diseased Single or Plain Parsley.—An experiment was conducted to determine whether the virus of western celery mosaic could be more readily recovered by mechanical inoculation or by means of noninfective aphids from Single or Plain parsley. Fifteen small plants were inoculated with the virus by the rusty-banded aphid. Three plants

developed symptoms of the disease and 12 plants failed to show symptoms on the leaves. The virus was recovered from only 7 of the 15 plants inoculated; the results obtained in the recovery of the virus by mechanical inoculation and by aphids are shown in table 3. According to these results, the virus was recovered from 6 plants by mechanical inoculation and from 2 plants by aphids. The 7 plants from which the virus was re-

TABLE 2

Comparative Infectiousness of Leaf Juice and Root Juice of Carrots Naturally and Experimentally Infected with Western Celery Mosaic

Type of infection and variety	Preparations used as sources of virus				Plants inoculated					
	Leaf juice		Root juice		With leaf juice		With root juice		Per cent infected	
	Number tested	Number infectious	Number tested	Number infectious	Number inoculated	Number infected	Number inoculated	Number infected	Leaf juice	Root juice
Natural										
Chantenay	2	0	2	2	10	0	10	9	0.0	90.0
Chantenay Red Cored	2	1	2	2	10	3	10	7	30.0	70.0
Danvers Half Long	2	1	2	2	10	4	10	5	40.0	50.0
Imperator	2	2	2	2	10	8	10	10	80.0	100.0
Short Top	2	2	2	2	10	3	10	7	30.0	70.0
Total, all varieties	10	6	10	10	50	18	50	38	36.0	76.0
Experimental										
Long Orange	5	5	5	5	25	18	25	24	72.0	96.0
Short White	5	4	5	4	25	13	25	15	52.0	60.0
White Belgian	5	4	5	5	25	8	25	24	32.0	96.0
Yellow Belgian	5	5	5	5	25	15	25	16	60.0	64.0
Total, all varieties	20	18	20	19	100	54	100	79	54.0	79.0

covered failed to show visible symptoms of the disease on the leaves. In this experiment, the virus was not recovered in either way from the 3 plants which showed symptoms of the disease. In other tests (not included in the table) the virus was recovered by both methods. It is evident that the virus was more readily recovered from Single or Plain parsley by mechanical inoculation than by aphids and also that some plants were symptomless carriers of the disease.

Attempts to Infect Cucumber Plants by Mechanical Inoculation.—Since celery has been reported to be susceptible to cucumber mosaic (cucumber virus 1) and southern celery mosaic is a strain of cucumber mosaic, attempts were made to transmit western celery mosaic to cucumber plants by mechanical inoculation of the expressed juice from nat-

urally infected celery collected in many different celery districts in California. In each test the juice was extracted from at least 5 naturally infected celery plants and inoculated in from 5 to 15 healthy celery and in the same number (with three exceptions) of White Spine cucumber plants. Frequently a celery plant was naturally infected by both western celery mosaic and celery calico, but the symptoms of celery calico were not conspicuous after secondary systemic symptoms of western celery mosaic developed on the older leaves. The expressed juice from a plant

TABLE 3

RECOVERY OF WESTERN-CELERY-MOSAIC VIRUS BY MECHANICAL INOCULATION AND BY RUSTY-BANDED APHID, *Aphis ferruginea-striata* ESSIG, FROM SINGLE OR PLAIN PARSLEY

Single or Plain parsley plant No.	Mechanically inoculated		Inoculated by *Aphis ferruginea-striata*	
	Celery plants		Celery plants	
	Inoculated	Infected	Inoculated	Infected
1	5	3	5	1
2	5	0	5	1
3	5	4	5	0
4	5	4	5	0
5	5	2	5	0
6	5	1	5	0
7	5	1	5	0
Total	35	15	35	2
Percentage	..	*42.9*	.....	*5.7*

containing the two viruses inoculated in healthy celery plants developed the typical symptoms of western celery mosaic on the inner leaves and celery calico on the outer leaves.

The results of inoculating healthy celery and cucumber plants with the extract from naturally infected celery plants are shown in table 4. Of the healthy celery plants inoculated with the extract from naturally infected celery collected in 23 celery districts, 53.8 per cent developed symptoms of western celery mosaic, while all of the cucumber plants inoculated remained healthy. Results of attempts to transmit the virus to cucumber plants by means of aphids are discussed on pages 521, 525-26.

When cucumber plants were inoculated with the extract from a naturally infected celery plant containing the two viruses, calico symptoms developed. When celery was inoculated with the expressed juice from these cucumbers, typical symptoms of celery calico developed on the

outer leaves but no symptoms of western celery mosaic appeared on the inner leaves. It is evident that the virus of celery calico was separated out of a virus complex in naturally infected celery by passage through cucumber and back to celery; the virus of western celery mosaic was filtered out.

TABLE 4

ATTEMPTS TO INFECT CUCUMBER PLANTS WITH EXTRACT FROM CELERY INFECTED WITH WESTERN CELERY MOSAIC COLLECTED IN MANY CELERY DISTRICTS OF CALIFORNIA

Source of virus		Date diseased celery collected	Control tests on celery plants		Cucumber plants	
County	District		Inoculated	Infected	Inoculated	Infected
Sacramento	Perkins	Aug. 10	5	5	5	0
	Sacramento Pocket	Sept. 10	5	5	5	0
Yolo	West Sacramento	Aug. 10	5	3	5	0
Contra Costa	San Pablo	July 26	5	1	5	0
San Mateo	Redwood City	July 8	5	5	5	0
Santa Clara	Palo Alto	April 29	5	1	5	0
		May 18	5	3	5	0
	Mountain View	April 10	5	4	5	0
		April 15	5	5	5	0
	Milpitas	April 8	10	8	10	0
		Sept. 17	5	4	5	0
Los Angeles	Baudin	Dec. 20	10	8	10	0
	Blue Hall	Dec. 20	10	7	10	0
	Compton	June 25	15	11	15	0
	Gardena	Nov. 13	30	24	30	0
		June 25	10	3	10	0
	Hawthorne	Dec. 6	5	2	5	0
	Lomita	June 25	15	5	15	0
	Malibu Beach	Dec. 8	10	5	10	0
	Moneta	Dec. 6	5	2	5	0
	San Fernando	Dec. 20	15	9	5	0
	Sawtelle	Dec. 6	10	3	10	0
	Venice	June 25	5	4	5	0
Orange	Santa Ana	Dec. 7	10	6	10	0
		June 28	20	1	15	0
	Seal Beach	Dec. 7	10	4	10	0
	Wintersburg	Dec. 7	10	6	10	0
San Diego	Chula Vista	June 30	10	1	5	0
		Dec. 5	15	3	15	0
Total			275	148	255	0
Percentage				*53.8*		*0.0*

PROPERTY STUDIES OF VIRUS

Filterability.—Filtration experiments were conducted by C. G. Weigle. The centrifuged extract from the leaves of celery naturally infected with western celery mosaic was filtered through Chamberland porcelain filters. One hour was allowed for the filtration at a negative pressure of 15–20 milligrams of mercury at room temperature. Six grades of Chamberland filters were used. The filtrates and unfiltered controls were inoculated in healthy celery. The results are shown in table 5. Western-

TABLE 5

FILTRATION OF WESTERN-CELERY-MOSAIC VIRUS THROUGH CHAMBERLAND PORCELAIN FILTERS

Filter No.	Experiment No. 1		Experiment No. 2		Experiment No. 3		Experiment No. 4		Total	
	Plants inoculated	Plants infected	Plants inoculated	Plants infected	Plants inoculated	Plants infected	Plants inoculated	Plants infected	Plants inoculated	Plants infected
L3	5	3	5	2	5	3	3	0	18	8
L5	5	1	5	3	5	2	3	0	18	6
L7	5	2	5	0	5	2	3	0	18	4
L9	5	0	5	1	..	..	..	..	10	1
L11	5	2	5	1	5	1	3	0	18	4
L13	5	1	5	0	5	1	3	0	18	2
Unfiltered control	5	3	5	2	..	..	6	2	16	7

celery-mosaic virus passed through all grades of Chamberland filters (L3, L5, L7, L9, L11, L13).

Thermal Inactivation.—The thermal inactivation of the western-celery-mosaic virus was determined in extracted juice from the leaves of naturally infected celery. Ten cc of diseased juice was poured into thin glass test tubes, which were then plugged with cotton and submerged in a water bath maintained at the desired temperature by an electric thermostat. The water was kept in circulation by an agitator connected to an electric motor. The time of exposure in the water bath was 11 minutes. About 1 minute was required for the heat to penetrate the glass test tube and bring the temperature of the extract to that of the constant-temperature water bath. After the exposure to the required temperature, the test tubes were cooled rapidly in running tap water. Unheated controls were used in each test. Determinations were made only at 5° C intervals. Table 6 shows that the diseased celery juice remained infective after heating at 55° C for 10 minutes, but the virus was inactivated at 60°.

Effect of Freezing Virus Extract.—The juice from the leaves of naturally infected celery was placed in cold storage at —18° C immediately after extraction. The number of infections obtained during a period of 18 months is shown in table 7. Freezing the extracted juice from diseased

TABLE 6

THERMAL INACTIVATION OF WESTERN-CELERY-MOSAIC VIRUS

Temperature, ° C	Preparations tested and found infectious		Celery plants inoculated and infected		
	Number tested	Number infectious	Number inoculated	Number infected	Per cent infected
Unheated	24	24	120	94	78.3
35	4	4	20	18	90.0
40	4	4	20	16	80.0
45	9	9	45	33	73.3
50	9	5	45	5	11.1
55	24	3	120	9	7.5
60	24	0	120	0	0.0
70	9	0	45	0	0.0

celery did not inactivate the virus of western celery mosaic at the end of 18 months.

Tolerance to Dilution.—The tolerance to dilution of the western-celery-mosaic virus was determined with the expressed juice from the leaves of naturally infected celery. The diluent consisted of sterile distilled

TABLE 7

INOCULATIONS OF HEALTHY CELERY WITH WESTERN-CELERY-MOSAIC JUICE KEPT IN COLD STORAGE AT —18° C

Age of virus extract, months	Plants infected (of 5 inoculated)	Age of virus extract, months	Plants infected (of 5 inoculated)
½	5	5	3
1	5	6	2
2	4	12	4
3	5	18	2
4	4		

water. The diluted juice was thoroughly agitated by pouring the solution back and forth in two beakers.

The results are shown in table 8. Western-celery-mosaic virus extracts showed a great variation in tolerance to dilution. The maximum tolerance of the virus to dilution demonstrated in extracted diseased celery juice was 1:4,000. With some of the preparations, infections were pro-

duced at a dilution of 1 : 10 or 1 : 50 but not at higher dilutions; this indicates a low concentration of virus.

Tolerance to Aging in Vitro.—Tests were made to determine the longevity of the virus in diseased celery juice when exposed to the air at

TABLE 8

TOLERANCE TO DILUTION OF WESTERN-CELERY-MOSAIC VIRUS

Dilution	Number of preparations infectious (of 12 tested)	Plants infected (of 60 inoculated)		Dilution	Number of preparations infectious (of 12 tested)	Plants infected (of 60 inoculated)	
		Number	Per cent			Number	Per cent
ControlNo.1*	12	40	66.7	ControlNo.2*	12	59	98.3
1:10	11	28	46.7	1:1,500	5	6	10.0
1:50	11	22	36.7	1:2,000	0	0	0.0
1:100	8	16	26.7	1:2,500	3	4	6.7
1:500	4	4	6.7	1:3,000	4	6	10.0
1:700	4	5	8.3	1:4,000	1	1	1.7
1:1,000	3	3	5.0	1:5,000	0	0	0.0

* Control No. 1 and dilutions from 1:10 to 1:1,000 were tested with one set of preparations; and control No. 2 with dilutions 1:1,500 to 1:5,000 with another set.

room temperatures. Ten cc of the expressed juice from the leaves of naturally infected celery was poured into sterile test tubes plugged with cotton. Daily inoculations of the extract stored *in vitro* were made for a period of 10 days.

The infections obtained are indicated in table 9. There is evidently

TABLE 9

TOLERANCE TO AGING IN VITRO OF WESTERN-CELERY-MOSAIC VIRUS

Days exposed	Number of preparations infectious (of 10 tested)	Plants infected (of 50 inoculated)		Days exposed	Number of preparations infectious (of 10 tested)	Plants infected (of 50 inoculated)	
		Number	Per cent			Number	Per cent
0 (control)	10	44	88.0	6	1	2	4.0
1	10	42	84.0	7	0	0	0.0
2	10	31	62.0	8	0	0	0.0
3	7	18	36.0	9	0	0	0.0
4	5	10	20.0	10	0	0	0.0
5	3	5	10.0				

considerable reduction of infectivity of the virus after the extract was stored *in vitro* at room temperature for a period of 4 to 6 days, and no infections were obtained at the end of 7 days.

Resistance to Alcohol Treatment.—In testing the effect of treatment with alcohol on diseased celery juice, small quantities of centrifuged juice were brought to various percentages of alcohol by the addition of

absolute alcohol, and the mixture was allowed to stand for a period of 1 hour. A precipitate was formed, which was separated from the supernatant liquid by centrifuging for 15 minutes at 3,500 revolutions per minute. The supernatant alcoholic solution was poured from the tubes. The precipitate was washed with several changes of sterile distilled water and then resuspended in distilled water equal to the original volume of the extracted celery juice.

The results of inoculating healthy celery plants with the supernatant liquid and the precipitate resuspended in distilled water are shown in table 10. The western-celery-mosaic virus in the supernatant liquid was

TABLE 10

Resistance of Western-Celery-Mosaic Virus Extract to Alcohol during One-Hour Exposures

Per cent alcohol	Number of preparations infectious (of 5 tested)		Plants infected (of 25 inoculated)			
			Number		Per cent	
	Supernatant liquid	Precipitate	Supernatant liquid	Precipitate	Supernatant liquid	Precipitate
0 (control).....	5	5	21	25	84.0	100.0
10.....	4	5	15	25	60.0	100.0
20.....	4	5	6	25	24.0	100.0
30.....	3	5	4	19	16.0	76.0
40.....	0	1	0	1	0.0	4.0
50.....	0	0	0	0	0.0	0.0

capable of withstanding treatment with 30 per cent alcohol, and the precipitate, treatment with 40 per cent alcohol for 1 hour. The resistance of the virus to alcohol in the supernatant and in the precipitate were probably equal. Most of the virus was apparently contained in the alcohol precipitate, and consequently a higher percentage of infections resulted from inoculations made from the precipitate.

INSECTS WHICH FAILED TO TRANSMIT VIRUS

High populations of beetles, plant bugs, and leafhoppers sometimes occur in celery fields, and tests were made to determine whether these insects could transmit the virus of western celery mosaic. The western twelve-spotted cucumber beetle (*Diabrotica soror* Lec.) and the tarnished plant bug (*Lygus pratensis* [Linn.]) were transferred frequently from diseased to healthy celery, back to diseased, and again to healthy celery plants but without results. Similar methods were used with several species of leafhoppers, using from 10 to 25 adults in each test, but all

attempts to transmit the virus were failures. Table 11 indicates the number of tests made with each species of insect: no infections were obtained with any of these insects.

Some of the leafhoppers are vectors of other virus diseases of celery. The aster leafhopper (*Macrosteles divisus* [Uhl.]) (*28*), the geminate leafhopper (*Thamnotettix geminatus* Van D.) (*30*), and the mountain leafhopper (*Thamnotettix montanus* Van D.) (*30*) have been reported as transmitting the virus of celery yellows, which is identical with California aster yellows. Celery has been experimentally infected with sugar-beet curly top by the beet leafhopper, *Eutettix tenellus* (Baker) (*28*).

TABLE 11

INSECTS THAT FAILED TO TRANSMIT WESTERN-CELERY-MOSAIC VIRUS

Insect	Celery plants	
	Inoculated	Infected
Western twelve-spotted cucumber beetle, *Diabrotica soror* Lec.	56	0
Tarnished plant bug, *Lygus pratensis* (Linn.)	100	0
Blue sharpshooter, *Cicadella circellata* (Baker)	25	0
Aster leafhopper, *Macrosteles divisus* (Uhl.)	25	0
Beet leafhopper, *Eutettix tenellus* (Baker)	25	0
Geminate leafhopper, *Thamnotettix geminatus* Van D.	25	0
Mountain leafhopper, *Thamnotettix montanus* Van D.	25	0

APHID TRANSMISSION OF VIRUS

Vectors Which Do Not Breed on Celery.—It was demonstrated that aphids which have not been found to breed on celery under natural conditions were capable of transmitting the virus of western celery mosaic. The mealy plum aphid (*Hyalopterus pruni* [Geoff.]) was transferred from the leaves of prune trees, the rose aphid (*Macrosiphum rosae* [Linn.]) from rose bushes, the black cherry aphid (*Myzus cerasi* [Fabr.]) from the leaves of cherry trees, to western-celery-mosaic plants for 1 day; and the next day 20 aphids were transferred to each healthy celery plant. In the case of the cabbage aphid (*Brevicoryne brassicae* [Linn.]), pea aphid (*Macrosiphum pisi* [Kalt.]), and the false cabbage or turnip aphid (*Lipaphis pseudobrassicae* [Davis]), previously noninfective aphids were used in the transmission of the virus. All species of aphids died on celery within a few days.

The results obtained are indicated in table 12. An examination of this table shows that the highest percentage of transmission of the western-celery-mosaic virus was by the cabbage aphid and the lowest by the mealy

plum and rose aphids. No determinations of different species of winged aphids in celery fields have been made, but large populations of winged aphids have been collected in the celery fields after the pasture vegetation on the foothills and the weeds in the cultivated areas had become dry. The influx of different species of winged aphids into celery fields, even if these are not able to breed on celery, probably plays an important rôle in the dissemination of the western-celery-mosaic virus.

Vectors Breeding on Celery.—Field investigations were conducted to

TABLE 12

TRANSMISSION OF WESTERN CELERY MOSAIC BY APHIDS THAT DO NOT BREED ON CELERY UNDER NATURAL CONDITIONS

Aphid	Celery plants		Per cent infected
	Inoculated	Infected	
Cabbage aphid, *Brevicoryne brassicae*, Linn.	35	27	77.1
Mealy plum aphid, *Hyalopterus pruni* (Geoff.)	75	7	9.3
Pea aphid, *Macrosiphum pisi* (Kalt.)	35	13	37.1
Rose aphid, *Macrosiphum rosae* (Linn.)	75	9	12.0
Black cherry aphid, *Myzus cerasi* (Fabr.)	35	15	42.9
False cabbage or turnip aphid, *Lipaphis pseudobrassicae* (Davis)	35	16	45.7

determine the aphids which breed on celery under natural conditions in California. The following species of aphids were reared on celery:

Celery leaf aphid, *Aphis apigraveolens* Essig (see Essig (7), fig. 1)
Celery aphid, *Aphis apii* Theobald (see Essig (7), fig. 2)
Rusty-banded aphid, *Aphis ferruginea-striata* Essig (see Essig (7), fig. 3)
Cotton or melon aphid, *Aphis gossypii* Glover (see Essig (7), fig. 4)
Erigeron root aphid, *Aphis middletonii* Thomas (see Essig (7), fig. 6)
Bean or dock aphid, *Aphis rumicis* Linnaeus
Yellow willow aphid, *Cavariella capreae* (Fabricius) (see Essig (7), fig. 7)
Lily aphid, *Myzus circumflexus* (Buckton) (see Essig (7), fig. 8)
Foxglove aphid, *Myzus convolvuli* (Kaltenbach) (see Essig (7), fig. 9)
Green peach aphid, *Myzus persicae* (Sulzer) (see Essig (7), fig. 11)
Honeysuckle aphid, *Rhopalosiphum melliferum* (Hottes) (see Essig (7), fig. 12)

The lily aphid has been taken on celery kept out of doors at Berkeley but has not been collected in celery fields up to the present time.

The rusty-banded aphid has been found feeding occasionally on the roots of celery, or on the base (stem) of the plant below the surface of the soil, but more often occurs between the petioles near the base of the plant and when abundant covers the petioles and veins of the leaves.

In the preceding paper, Essig (7) reports that the erigeron root aphid feeds on the roots of asters and on a wide range of other plants in Cali-

fornia. It has been found on the roots of celery near Chula Vista, San Diego County, and in the Santa Clara Valley.

Some species of aphids become abundant in celery fields during certain seasons of the year. The cotton or melon aphid was abundant on celery in the Santa Clara Valley on July 8, 1935; but this aphid when reared on celery in the greenhouse becomes greatly reduced in size and the populations are slow to develop. The green peach aphid was numerous on celery in the Santa Clara Valley on December 19, 1935, and yet this aphid was difficult to rear on celery in the greenhouse. An enormous number of host plants of some of these aphids is discussed by Essig (7) in the preceding paper, and in all probability the abundance of some species of aphids on celery during certain seasons of the year hinges on the drying of some of their breeding plants.

Transmission of Virus by Different Species of Aphids.—Celery infected with western celery mosaic was shipped by plant pathologists, county agents, and growers and was collected by the writers from many celery districts in California to determine the distribution and relative importance of different species of aphids and whether a specific vector was transmitting the virus.

The diseased plants were transplanted in pots enclosed in cages and the aphids were allowed to multiply on the plants. High populations of aphids were used in each test, but no accurate count of the number of aphids was made; the leaves with the aphids were cut from the diseased plant and dropped on the leaves or between the petioles of the healthy plants.

Table 13 gives the number of infections obtained with the different species of aphids. An examination of the average percentages of celery plants infected by different species of aphids in this table shows that the bean or dock aphid and the yellow willow aphid were not efficient vectors of the virus.

Attempts to Transmit Virus to Cucumber Plants by Means of Aphids.—The results of mechanical inoculation of healthy celery and cucumber plants with the extract from celery infected with western celery mosaic collected in many celery districts in California are given in table 4 (p. 514) and have been discussed under the heading of inoculation experiments. Attempts were made to transmit the virus from naturally infected celery with 11 species of aphids to healthy celery and the cucumber plants. Celery plants showing leaf abnormalities, such as club-shaped leaves (fig. 5, p. 506), linear leaflets (plate 6, *A, B, E, F*) or blisterlike pustules on the leaflets (plate 6, *D*), were also tested. Previously noninfective aphids reared on celery naturally infected with western celery mosaic and on

TABLE 13

TRANSMISSION OF WESTERN-CELERY-MOSAIC VIRUS BY DIFFERENT SPECIES OF APHIDS FROM DISEASED TO HEALTHY CELERY

Source of virus		Dates aphids inoculated plants	Plants inoculated	Plants infected
County	District			
Celery leaf aphid, *Aphis apigraveolens* Essig				
Los Angeles	San Fernando	Feb. 3–6	5	5
	Long Beach	Feb. 5–8	5	5
	Sawtelle	Feb. 5–8	5	5
Orange	Santa Ana	Feb. 5–8	5	4
Sacramento	Sacramento Pocket	Mar. 2–5	5	3
Total			25	22
Percentage			....	*88.0*
Celery aphid, *Aphis apii* Theobald				
Los Angeles	Gardena	Oct. 26–Nov. 5	19	9
Santa Clara	Mountain View	Oct. 15–22	5	5
		Oct. 16–22	1	1
	Palo Alto	Sept. 28–Oct. 8	10	7
		Oct. 5–11	10	8
		Oct. 12–15	10	7
		Oct. 12–18	5	3
		Oct. 15–22	10	10
San Mateo	Redwood City	Oct. 15–22	5	5
		Oct. 16–22	5	5
Total			80	60
Percentage			....	*75.0*
Rusty-banded aphid, *Aphis ferruginea-striata* Essig				
Los Angeles	Gardena	Aug. 24–Sept. 2	12	11
		Aug. 30–Sept. 7	6	6
		Sept. 5–18	6	2
		Sept. 13–26	18	6
		Sept. 14–26	1	1
		Sept. 18–27	12	6
		Oct. 2–12	3	3
		Oct. 12–15	10	10
Santa Clara	Palo Alto	Oct. 5–16	1	1
Total			69	46
Percentage			....	*66.7*

TABLE 13—(*Continued*)

Source of virus		Dates aphids inoculated plants	Plants inoculated	Plants infected
County	District			
Cotton or melon aphid, *Aphis gossypii* Glover				
Los Angeles	Gardena	Feb. 19–March 1	10	6
		Apr. 24–30	5	3
Santa Clara	Mountain View	Mar. 7–12	5	5
		Mar. 11–20	10	7
		Mar. 11–19	5	4
		Mar. 12–19	5	4
		Mar. 15–22	10	10
		Mar. 20–Apr. 3	5	2
		Mar. 25–Apr. 2	5	5
		Mar. 29–Apr. 3	5	3
		Apr. 4–9	5	4
		May 3–8	10	8
	Palo Alto	Mar. 7–10	5	5
Total			85	66
Percentage				*77.6*
Erigeron root aphid, *Aphis middletonii* Thomas				
Santa Clara	Milpitas	Aug. 5–8	12	11
		Aug. 17–20	4	3
		Aug. 19–22	16	14
		Aug. 22–26	5	4
		Aug. 23–26	10	10
Total			47	42
Percentage				*89.4*
Bean or dock aphid, *Aphis rumicis* Linn.				
Santa Clara	Milpitas	May 1–7	10	1
		May 5–9	25	7
	Palo Alto	Sept. 17 Oct. 3	10	1
Total			45	9
Percentage				*20.0*
Yellow willow aphid, *Cavariella capreae* (Fabr.)				
Los Angeles	Bassett	Jan. 8–11	5	4
	Compton	Jan. 9–13	5	1
	San Fernando	Jan. 9–13	5	1
		Mar. 9–12	5	2
Sacramento	Perkins	Mar. 9–12	5	2
Orange	Santa Ana	Mar. 9–12	5	1
Total			30	11
Percentage				*36.7*

TABLE 13—(*Concluded*)

Source of virus		Dates aphids inoculated plants	Plants inoculated	Plants infected
County	District			
Lily aphid, *Myzus circumflexus* (Buck.)				
Los Angeles	Gardena	Sept. 12–22	6	2
		Sept. 14–26	12	6
		Oct. 9–15	10	6
		Oct. 11–15	20	9
		Oct. 25–Nov. 2	10	5
Total			58	28
Percentage				*48.3*
Foxglove aphid, *Myzus convolvuli* (Kalt.)				
Santa Clara	Milpitas	Sept. 2–7	5	3
	San Jose	Sept. 30–Oct. 2	5	3
	Palo Alto	Sept. 30–Oct. 2	5	3
Sacramento	Perkins	Sept. 16–18	5	5
	Sacramento Pocket	Sept. 16–18	5	4
Total			25	18
Percentage				*72.0*
Green peach aphid, *Myzus persicae* (Sulz.)				
Los Angeles	Gardena	Sept. 14–22	6	1
		Oct. 17–21	3	1
Santa Clara	Milpitas	Apr. 23–27	6	5
		May 30–June 3	10	5
		Aug. 19–29	10	10
		Aug. 26–31	10	8
	Mountain View	Jan. 31–Feb. 5	10	6
		Feb. 13–18	5	2
		Feb. 21–26	3	1
		Aug. 26–31	5	2
Total			68	41
Percentage				*60.3*
Honeysuckle aphid, *Rhopalosiphum melliferum* (Hottes)				
Los Angeles	Gardena	Nov. 7–16	55	36
Santa Clara	Milpitas	Aug. 12–15	10	10
		June 7–14	12	11
	Mountain View	July 6–10	10	10
		Oct. 5–10	2	2
		Oct. 26–30	5	4
	Palo Alto	June 19–25	10	0
Total			104	73
Percentage				*70.2*

celery showing leaf abnormalities were transferred from each diseased celery to 5 healthy celery and 5 White Spine cucumber plants.

The results obtained are given in table 14. None of the 11 species of aphids transmitted the virus of western celery mosaic from any of the naturally infected celery plants to any of the healthy cucumber plants.

The rusty-banded aphid and the erigeron root aphid were the most efficient vectors of these species, the former infecting an average of 92 per cent and the latter 90 per cent of the healthy celery plants. Least efficient was the bean or dock aphid, which transmitted the virus to 1 of 5 healthy celery plants from 1 naturally infected plant.

Some of the celery plants with abnormal leaves were demonstrated to be naturally infected with western celery mosaic.

Comparison of Mechanical Inoculation with Transmission of Virus by Aphids.—Mechanical inoculation was compared with the transmission of the western-celery-mosaic virus by different species of aphids from naturally infected to healthy celery plants. After a large population of aphids were reared on the naturally infected celery plants, 20 aphids were transferred from each diseased plant to each of 5 healthy celery plants. The extract from each naturally infected plant, on which the aphids had fed, was also inoculated into 5 healthy celery plants.

A comparison of the results obtained is given in table 15. The transmission of the virus from diseased to healthy celery by 11 species of aphids varied from 2.2 to 92.5 per cent. Nine lots of 20 bean or dock aphids infected only 1 of 45 plants, or 2.2 per cent, whereas with mechanical inoculation of expressed juice from the same naturally infected plants on which these aphids had fed, 40 of 45 celery plants, or 88.9 per cent, became infected. If the results with the bean or dock aphid are omitted, the transmission of the virus by 10 species of aphids varied from 35.0 to 92.5 per cent. The infections obtained by mechanical inoculation varied from 13.3 to 88.9 per cent, with an average of 48.2 per cent; this is somewhat lower than the average of 53.8 per cent obtained in the experiments reported in table 4.

Detailed records not included in table 15 indicate that infections were obtained, either by mechanical inoculation or aphid transmission from each of the naturally infected plants used as a source of virus; in no case did both methods fail. As indicated in table 15, six species of aphids obtained the infection from all of the naturally infected plants on which they fed, but the bean or dock aphid obtained it from only 1 of 9 plants; the results with other species were intermediate. Preparation of juice from 23 of the 102 plants failed to transmit the virus when mechanically inoculated.

TABLE 14

ATTEMPTS TO INFECT CUCUMBER PLANTS WITH WESTERN-CELERY-MOSAIC VIRUS BY MEANS OF VARIOUS SPECIES OF APHIDS

Aphid	Naturally infected celery plants			Control tests with celery plants			Cucumber plants tested		
	Plants tested	Number from which infections were obtained		Number inoculated	Number infected	Per cent infected	Number inoculated	Number infected	Per cent infected
		To celery	To cucumber						
Celery leaf aphid, *Aphis apigraveolens* Essig	5	5	0	25	12	48.0	25	0	0.0
Celery aphid, *Aphis apii* Theobald	5	5	0	25	15	60.0	25	0	0.0
Rusty-banded aphid, *Aphis ferruginea-striata* Essig	5	5	0	25	23	92.0	25	0	0.0
Cotton or melon aphid, *Aphis gossypii* Glover	5	5	0	25	15	60.0	25	0	0.0
Erigeron root aphid, *Aphis middletonii* Thomas	6	6	0	30	27	90.0	30	0	0.0
Bean or dock aphid, *Aphis rumicis* Linn.	1	1	0	5	1	20.0	5	0	0.0
Yellow willow aphid, *Cavariella capreae* (Fabr.)	5	5	0	25	14	56.0	25	0	0.0
Lily aphid, *Myzus circumflexus* (Buck.)	6	6	0	30	24	80.0	30	0	0.0
Foxglove aphid, *Myzus convolvuli* (Kalt.)	5	5	0	25	17	68.0	25	0	0.0
Green peach aphid, *Myzus persicae* (Sulz.)	5	5	0	25	21	84.0	25	0	0.0
Honeysuckle aphid, *Rhopalosiphum melliferum* (Hottes)	6	6	0	30	16	53.3	30	0	0.0

TABLE 15

COMPARISON OF TRANSMISSION OF WESTERN-CELERY-MOSAIC VIRUS BY MECHANICAL INOCULATION WITH DIFFERENT SPECIES OF APHIDS FROM NATURALLY INFECTED TO HEALTHY CELERY PLANTS

Number of plants from which virus was obtained	Mechanical inoculation				Aphid transmission				
	Preparations infectious	Celery plants			Aphid	Plants proved infectious	Celery plants		
		Inoculated	Infected	Per cent infected			Inoculated	Infected	Per cent infected
12	12	60	51	85.0	Celery leaf aphid, *Aphis apigraveolens* Essig	11	60	42	70.0
7	5	35	15	42.9	Celery aphid, *Aphis apii* Theobald	6	35	20	57.1
8	5	40	11	27.5	Rusty-banded aphid, *Aphis ferruginea-striata* Essig	8	40	37	92.5
5	3	25	6	24.0	Cotton or melon aphid, *Aphis gossypii* Glover	5	25	15	60.0
10	10	50	29	58.0	Erigeron root aphid, *Aphis middletonii* Thomas	10	50	42	84.0
9	9	45	40	88.9	Bean or dock aphid, *Aphis rumicis* Linn	1	45	1	2.2
8	7	40	19	47.5	Yellow willow aphid, *Cavariella capreae* (Fabr.)	5	40	14	35.0
6	2	30	4	13.3	Lily aphid, *Myzus circumflexus* (Buck.)	6	30	24	80.0
14	8	70	23	32.9	Foxglove aphid, *Myzus convolvuli* (Kalt.)	14	70	33	47.1
17	15	85	41	48.2	Green peach aphid, *Myzus persicae* (Sulz.)	14	85	45	52.9
6	3	30	7	23.3	Honeysuckle aphid, *Rhopalosiphum melliferum* (Hottes)	6	30	24	80.0
102	79	510	246	48.2		..	..	..	....

Summary of Transmission of Virus by Aphids Breeding on Celery.—The average percentages of infections obtained with 11 species of aphids are summarized in table 16. The erigeron root aphid (84.8 per cent) and the rusty-banded aphid (83.8 per cent), also a root-feeding insect, produced the largest number of infections, with the honeysuckle aphid (73.4 per cent), lily aphid (72.1 per cent), cotton or melon aphid (71.4 per cent), celery leaf aphid (64.5 per cent), green peach aphid (62.6 per cent), celery aphid (58.0 per cent), and foxglove aphid (55.9 per cent)

TABLE 16

Summary of Percentages of Infections Produced by Different Species of Aphids

Aphid	Table 13	Table 14	Table 15	Table 18	Average percentage
Celery leaf aphid, *Aphis apigraveolens* Essig	88.0	48.0	70.0	52.0	64.5
Celery aphid, *Aphis apii* Theobald	75.0	60.0	57.1	40.0	58.0
Rusty-banded aphid, *Aphis ferruginea-striata* Essig	66.7	92.0	92.5	84.0	83.8
Cotton or melon aphid, *Aphis gossypii* Glover	77.6	60.0	60.0	88.0	71.4
Erigeron root aphid, *Aphis middletonii* Thomas	89.4	90.0	84.0	76.0	84.8
Bean or dock aphid, *Aphis rumicis* Linn.	20.0	20.0	2.2	....	14.1
Yellow willow aphid, *Cavariella capreae* (Fabr.)	36.7	56.0	35.0	32.0	39.9
Lily aphid, *Myzus circumflexus* (Buck.)	48.3	80.0	80.0	80.0	72.1
Foxglove aphid, *Myzus convolvuli* (Kalt.)	72.0	68.0	47.1	36.7	55.9
Green peach aphid, *Myzus persicae* (Sulz.)	60.3	84.0	52.9	53.3	62.6
Honeysuckle aphid, *Rhopalosiphum melliferum* (Hottes)	70.2	53.3	80.0	90.0	73.4

next in order. The rusty-banded aphid is the most important vector of the virus of western celery mosaic in California when distribution and abundance on celery are considered. The bean or dock aphid (8.6 per cent) and the yellow willow aphid (14.1 per cent) produced the lowest percentages of infections. It is evident from the high percentages of transmission of the virus by various species of aphids, that *there is no specific aphid vector.*

Transmission of Virus by Single Aphids.—A comparison was made of the transmission of the western-celery-mosaic virus by single winged and wingless mature aphids bred on diseased plants. Each aphid was fed on a healthy celery plant for a period of 1 day.

The results obtained are indicated in table 17. Considerable variation occurred in the ability of single aphids of different species to infect plants. The winged aphids, with the exception of one species, transmitted the virus to a lower percentage of plants than the wingless mature aphids. The highest percentage by single wingless mature aphids was 37.3, produced by the rusty-banded aphid, while the winged forms of this species

infected 2.0 per cent of the plants. The highest percentage of infection by single winged aphids was 7.0, produced by the celery leaf aphid, as compared with 14 per cent by the wingless mature aphids. The lowest percentages of infections were produced by the celery aphid, green peach aphid, and the foxglove aphid.

Retention of Virus by Aphids.—Four experiments were conducted to determine how long aphids would retain the virus. In the first of these, wingless aphids of ten species were transferred daily to successive

TABLE 17

COMPARISON OF TRANSMISSION OF WESTERN-CELERY-MOSAIC VIRUS BY SINGLE WINGED WITH WINGLESS MATURE APHIDS FROM DISEASED TO HEALTHY CELERY PLANTS

Aphid	Results with winged aphids			Results with wingless mature aphids		
	Plants inoculated	Plants infected	Percent infected	Plants inoculated	Plants infected	Percent infected
Celery leaf aphid, *Aphis apigraveolens* Essig	100	7	7.0	100	14	14.0
Celery aphid, *Aphis apii* Theobald	100	0	0.0	200	3	1.5
Rusty-banded aphid, *Aphis ferruginea-striata* Essig	100	2	2.0	150	56	37.3
Cotton or melon aphid, *Aphis gossypii* Glover	100	4	4.0	100	8	8.0
Erigeron root aphid, *Aphis middletonii* Thomas	100	3	3.0	300	10	3.3
Yellow willow aphid, *Cavariella capreae* (Fabr.)	100	0	0.0	200	5	2.5
Lily aphid, *Myzus circumflexus* (Buck.)	0	0	0.0	150	12	8.0
Foxglove aphid, *Myzus convolvuli* (Kalt.)	100	1	1.0	100	0	0.0
Green peach aphid, *Myzus persicae* (Sulz.)	100	0	0.0	150	1	0.7
Honeysuckle aphid, *Rhopalosiphum melliferum* (Hottes)	100	3	3.0	215	19	8.8

healthy celery plants, 5 or 6 tests being made with each species. In each test, 20 aphids reared on diseased celery were transferred daily for 3 days to successive healthy celery plants. The aphids remained on the third celery plant for a period of one week.

The results obtained are indicated in table 18. Each of ten species of aphids transmitted the virus from diseased to healthy celery plants during the first day, but every one of the lots tested had lost the infectivity by the second day—no transmissions were obtained after the first day under greenhouse conditions. It is possible, however, that with a lowering of the temperature during the winter the aphids may retain the infectivity longer than one day under natural conditions.

In the second experiment, 20 wingless adults of the rusty-banded aphid reared on diseased celery were fed overnight on a healthy celery plant for a period of 12 hours. During the next day, the aphids were transferred hourly to 8 successive healthy celery plants. Each lot of 20

TABLE 18

RETENTION OF WESTERN-CELERY-MOSAIC VIRUS BY 10 SPECIES OF APHIDS TRANSFERRED DAILY TO THREE SUCCESSIVE HEALTHY CELERY PLANTS

Aphid	Aphid lots (20 each) tested				Celery plants inoculated				
	Number lots tested	Number transmitting virus			Number inoculated each day	Number infected 1st day	Per cent infected		
		1st day	2d day	3d–9th day			1st day	2d day	3d–9th day
Celery leaf aphid, *Aphis apigraveolens* Essig	5	5	0	0	25	13	52.0	0.0	0.0
Celery aphid, *Aphis apii* Theobald	5	5	0	0	25	10	40.0	0.0	0.0
Rusty-banded aphid, *Aphis ferruginea-striata* Essig	5	5	0	0	25	21	84.0	0.0	0.0
Cotton or melon aphid, *Aphis gossypii* Glover	5	5	0	0	25	22	88.0	0.0	0.0
Erigeron root aphid, *Aphis middletonii* Thomas	5	5	0	0	25	19	76.0	0.0	0.0
Yellow willow aphid, *Cavariella capreae* (Fabr.)	5	5	0	0	25	8	32.0	0.0	0.0
Lily aphid, *Myzus circumflexus* (Buck.)	5	5	0	0	25	20	80.0	0.0	0.0
Foxglove aphid, *Myzus convolvuli* (Kalt.)	6	6	0	0	30	11	36.7	0.0	0.0
Green peach aphid, *Myzus persicae* (Sulz.)	9	9	0	0	45	24	53.3	0.0	0.0
Honeysuckle aphid, *Rhopalosiphum melliferum* (Hottes)	6	6	0	0	30	27	90.0	0.0	0.0

TABLE 19

RETENTION OF WESTERN-CELERY-MOSAIC VIRUS BY 20 APHIDS TRANSFERRED HOURLY TO 10 SUCCESSIVE HEALTHY CELERY PLANTS

Aphid	Number of aphids on first plant	Results* on successive plants, with hourly transfers										Last infection produced by aphids, hour
		1st	2d	3d	4th	5th	6th	7th	8th	9th	10th	
Rusty-banded aphid, *Aphis ferruginea-striata* Essig	20	+	−	−	−	−	−	−	−	−	−	1st
	20	+	−	−	−	−	−	−	−	−	−	1st
	20	+	−	−	−	−	−	−	−	−	−	1st
	20	+	−	+	−	−	−	−	−	−	−	3d
	20	+	−	−	+	−	−	−	−	−	−	4th
	20	−	−	−	−	−	+	−	−	−	−	6th
	20	−	−	−	−	−	−	+	+	−	−	8th
	20	−	−	−	−	−	−	−	−	−	+	10th
Erigeron root aphid, *Aphis middletonii* Thomas	20	+	−	−	−	−	−	−	−	−	−	1st
Honeysuckle aphid, *Rhopalosiphum melliferum* (Hottes)	20	+	−	−	−	−	−	−	−	−	−	1st
Total +	.....	7	0	1	1	0	1	1	1	0	1	....
Total −	.....	3	10	9	9	10	9	9	9	10	9	....

* The plus sign (+) indicates the production of the disease, and the minus sign (−) shows that no disease resulted.

aphids infected the first set of healthy celery plants, on which they were kept for a period of 12 hours, but had lost the infective dose of the virus when transferred to the second set of healthy plants; no subsequent transmissions were obtained.

In the third experiment, 10 lots of 20 wingless aphids reared on diseased celery were transferred hourly with a moistened camel's-hair brush to 10 successive healthy celery plants. Eight lots of the rusty-banded aphids and 1 lot each of the erigeron root aphid and the honeysuckle aphid were tested. The mortality was low with the three species of aphids selected. As shown in table 19, 3 of the rusty-banded and 1 each of the other two species of aphids infected a celery plant during the first hour only, 2 lots infected plants during the first hour and again during the third or fourth hour, one lot infected a plant during the sixth hour, another lot infected 2 successive plants during the seventh and eighth hours only, and lastly 1 lot infected a plant during the tenth hour only.

In the last experiment, 18 single noninfective aphids were fed for varying periods on diseased celery and then each aphid was transferred hourly for a period of 8 hours and then daily until it died to successive healthy celery plants. The work with single aphids required many tests, most of which were negative. The positive results obtained with 10 different species of aphids during the hourly transfers are given in table 20. Four of the aphids infected only the first celery plant and then lost the infective power; 3 aphids infected the first plant, retained the infective dose of the virus, and infected a second plant. One erigeron root aphid (*Aphis middletonii*) infected celery plants during the fifth and eighth hours, retaining the virus 7 to 8 hours. The ten species of aphids transferred daily to healthy celery plants failed to infect a single plant. Some of the aphids died during the first day, others were transferred daily to healthy plants for over a month. One lily aphid was transferred daily to successive healthy celery plants for a period of 38 days.

Loss and Recovery of Infectivity by Aphids on Infected Plants.—Since many growers rogue diseased celery from their fields, an attempt was made to determine whether different species of aphids were able to recover the virus from infected celery before the first symptom of the disease developed. A large population of aphids reared on a diseased celery plant was transferred to a healthy celery plant for 2 days. For a period of 12 days from the third to the fourteenth day, lots of 20 of these aphids were transferred daily from the plant so infected to healthy celery plants.

The loss and recovery of infectivity by aphids on celery inoculated with western celery mosaic and the incubation period of the disease or

TABLE 20

RETENTION OF WESTERN-CELERY-MOSAIC VIRUS BY SINGLE APHIDS TRANSFERRED HOURLY TO 8 SUCCESSIVE HEALTHY CELERY PLANTS

Aphid	Length of time on diseased plants, hours	Results* on successive plants with hourly transfers								Last infection produced by aphids, hour
		1st	2d	3d	4th	5th	6th	7th	8th	
Celery leaf aphid, *Aphis apigraveolens* Essig	2	+	−	−	−	−	−	−	−	1st
	1	−	−	+	−	−	−	−	−	3d
Celery aphid, *Aphis apii* Theobald	1	−	−	−	−	−	+	−	−	6th
Rusty-banded aphid, *Aphis ferruginea-striata* Essig	2	+	−	−	−	−	−	−	−	1st
Cotton or melon aphid, *Aphis gossypii* Glover	2	−	+	−	−	−	−	−	−	2d
Erigeron root aphid, *Aphis middletonii* Thomas	2	+	−	−	−	−	−	−	−	1st
	3	−	−	−	−	+	−	−	+	8th
Yellow willow aphid, *Cavariella capreae* (Fabr.)	24	−	−	−	+	−	−	−	−	4th
	3	+	−	+	−	−	−	−	−	3d
	3	−	−	−	−	+	−	−	−	5th
Lily aphid, *Myzus circumflexus* (Buck.)	1	+	−	−	−	+	−	−	−	5th
	1	−	−	+	−	−	−	−	−	3d
Foxglove aphid, *Myzus convolvuli* (Kalt.)	2	+	−	−	−	−	−	−	−	1st
	3	−	−	−	−	−	−	+	−	7th
Green peach aphid, *Myzus persicae* (Sulz.)	2	−	−	−	−	−	−	+	−	7th
Honeysuckle aphid, *Rhopalosiphum melliferum* (Hottes)	3	+	+	−	−	−	−	−	−	2d
	3	−	+	−	−	−	−	−	−	2d
	1	−	−	−	+	−	−	−	−	4th
Total +	....	7	3	3	2	3	1	2	1	....
Total −	....	11	15	15	16	15	17	16	17	....

* The plus sign (+) indicates the production of the disease, and the minus sign (−) shows that no disease resulted.

TABLE 21

LOSS AND RECOVERY OF INFECTIVITY BY APHIDS ON CELERY INOCULATED WITH WESTERN-CELERY-MOSAIC VIRUS

Aphid	Original plant number	Elapsed time after aphids inoculated each healthy celery plant for 2 days and then lots of 20 aphids were transferred daily to healthy plants												Days to the first symptom on original plants
		3	4	5	6	7	8	9	10	11	12	13	14	
Celery leaf aphid, *Aphis apigraveolens* Essig	1	−	−	−	−	−	−	−	−	−	−	+	−	10
	2	−	−	−	−	−	−	−	−	−	−	−	+	12
Celery aphid, *Aphis apii* Theobald	3	−	−	−	−	−	−	−	−	+	+	+	+	8
Rusty-banded aphid, *Aphis ferruginea-striata* Essig	4	−	−	−	+	−	+	−	−	−	−	−	−	9
	5	−	−	−	+	−	−	−	+	+	−	+	−	4
	6	−	−	−	−	−	+	−	+	−	+	+	+	8
	7	−	−	−	−	−	−	+	+	+	+	−	−	9
	8	−	−	−	−	−	−	+	−	+	+	−	−	9
	9	−	−	−	−	−	−	−	+	−	−	−	−	5
	10	−	−	−	−	−	−	−	+	+	−	+	+	8
	11	−	−	−	−	−	−	−	+	−	+	+	−	4
	12	−	−	−	−	−	−	−	−	+	+	+	+	8
	13	−	−	−	−	−	−	−	−	−	+	+	−	8
Cotton or melon aphid, *Aphis gossypii* Glover	14	−	−	−	−	−	−	−	+	−	−	−	−	4
	15	−	−	−	−	−	−	−	+	+	−	−	−	6
Erigeron root aphid, *Aphis middletonii* Thomas	16	−	−	−	−	−	+	−	−	−	−	−	−	11
	17	−	−	−	−	−	+	−	−	−	−	−	+	6
	18	−	−	−	−	−	−	−	−	−	+	−	−	12
	19	−	−	−	−	−	−	−	−	−	−	+	−	9
Yellow willow aphid, *Cavariella capreae* (Fabr.)	20	−	−	−	−	−	−	−	−	−	−	+	−	10
	21	−	−	−	−	+	−	−	+	−	−	+	+	9

TABLE 21—(*Concluded*)

Aphid	Original plant number	Elapsed time after aphids inoculated each healthy celery plant for 2 days and then lots of 20 aphids were transferred daily to healthy plants												Days to the first symptom on original plants
		3	4	5	6	7	8	9	10	11	12	13	14	
Lily aphid, *Myzus circumflexus* (Buck.)	22	–	–	–	–	–	–	+	–	+	–	–	–	6
	23	–	–	–	–	–	–	–	–	+	–	+	–	8
	24	–	–	–	–	–	–	–	–	–	+	–	–	9
	25	–	–	–	–	–	–	–	–	–	–	+	+	9
	26	–	–	–	–	–	–	–	–	–	–	+	–	8
	27	–	–	–	–	–	–	–	–	–	–	+	–	8
	28	–	–	–	–	–	–	–	–	–	–	–	+	16
	29	–	–	–	–	–	–	–	–	–	–	–	+	9
Foxglove aphid, *Myzus convolvuli* (Kalt.)	30	–	–	–	–	–	+	–	–	–	–	–	–	7
	31	–	–	–	–	–	–	–	–	+	–	+	–	7
Honeysuckle aphid, *Rhopalosiphum melliferum* (Hottes)	32	–	–	–	–	–	+	–	–	–	–	+	–	9
	33	–	–	–	–	–	+	–	–	–	–	–	–	9
	34	–	–	–	–	–	–	+	–	+	+	–	+	9
	35	–	–	–	–	–	–	–	+	+	+	–	–	8
	36	–	–	–	–	–	–	–	–	+	–	–	–	10
	37	–	–	–	–	–	–	–	–	–	–	+	–	9
Total +		0	0	0	2	1	7	4	10	13	11	18	11	
Total −		37	37	37	35	36	30	33	27	24	26	19	26	

* The plus sign (+) indicates the production of the disease, and the minus sign (−) shows that no disease resulted.

the period for the earliest symptom to develop, namely the cleared veinlets in the original infected celery plant, are shown in table 21. The elapsed time to the first recovery of the virus by different species of aphids from the original infected celery plants varied from 6 to 14 days. The incubation period of the disease in the original infected celery plants varied from 4 to 16 days. A comparison of the first recovery of the virus by lots of 20 aphids with the incubation period of the disease in the original infected celery plants shows that 6 of 37 lots of aphids recovered the virus before symptoms of the disease developed, 5 lots recovered the virus on the same day that the earliest symptom of the disease appeared, and 26 lots recovered the virus in from 1 to 6 days after the earliest symptom of the disease developed. An examination of the total number of positives shows that the maximum period of recovery of the virus by aphids occurred between 10 and 14 days.

CONTROL

Celery-Free Periods.—Milbrath (*18, 19, 20*) claims that a celery-free period, adopted by agreement with the growers, has proved a practical method of combating celery mosaic in the Sawtelle and Venice districts.

TABLE 22

Celery-Free Periods in the Fields and Greenhouses in the Sawtelle and Venice Districts, Los Angeles County*

Year	Celery-free period in fields		Celery-free period in greenhouses	
	Dates	Months	Dates	Months
1934	July 31 to Jan. 1	5	Sept. 1 to Oct. 20	1⅔
1935	Aug. 31 to Dec. 20	3⅔	Sept. 15 to Oct. 15	1
1936	Sept. 16 to Dec. 11	3⅔	Sept. 16 to Oct. 16	1

*Source of data:
Milbrath, D. G., and Harold J. Ryan. A method of control of western celery mosaic. California State Dept. Agr. Mo. Bul. 27 (3): 290-95. 1938.

During the past three years, growers were prohibited from planting celery in the fields and greenhouses during the periods indicated in table 22.

During the celery-free period, all fields in the restricted area were plowed, and all plants not previously harvested were destroyed. No celery was allowed to be shipped into these districts from other localities during the celery-free period. The crops grown after the celery-free period thus far have shown tremendous improvement, and the growers are well satisfied, according to H. H. Wilcomb (Schraff, *27*), who was in charge of control of celery mosaic in Los Angeles County, and also to Milbrath (*18, 19, 20*) and Brock (*2*).

Macmillan and Plunkett (*59*) reported their observations on western celery mosaic during the 1937 celery-growing season in the southern part of California. In the Venice section on May 25, in "fields approaching harvest mosaic is general and severe." On June 18, mosaic "varied widely from field to field, some having as much as 50 per cent severely infected plants." On August 13, "mosaic is common in the field." On September 16, celery "plants about 6 inches high showed 80 per cent infection with mosaic throughout several fields near Redondo." No case of mosaic was observed on wild or escaped celery growing in the Los Angeles River bottom and in marshy places in valley bottoms, and in desert surroundings in San Diego County where seepage supplies constant water.

Observations in Santa Clara Valley indicate that celery plants may show a high percentage of disease and yet make a profitable crop. The percentage of diseased plants is of little economic importance if celery plants are infected when large. Small celery plants showing 80 per cent infection at Redondo would result in a loss or total failure, but Redondo is outside of the restricted area in which the celery-free period has been reported as a success in combating western celery mosaic. According to table 1 (p. 495), the yield per acre was increased during 1936 and 1937 after the adoption of the celery-free period in the Venice and Culver districts.

Planting Time.—Ryan (*25*) reported that many fields were 100 per cent infected with western celery mosaic in the Venice district in the fall of 1932, and that during the spring of 1934 celery was a total failure because of the disease.

Observations in the Santa Clara Valley indicate that celery grown in the greenhouse and transplanted in the field in March showed a low percentage of diseased plants when harvested in June. When low temperatures prevailed, however, early-planted celery often developed seedstalks. Celery transplanted during April and May showed a high percentage of infected plants when harvested during July and August. Successive plantings of celery showed a gradual increase in the percentage of diseased plants during late spring and early summer. Celery transplanted during August and September, on the other hand, was not usually seriously affected with the disease unless it was grown adjacent to celery which showed a high percentage of infected plants. Celery transplanted adjacent to larger plants which showed a high percentage of infected plants usually results in a loss.

The fact that celery which matures in July and August is usually severely damaged has suggested a celery-free period during these two months in the Santa Clara Valley. Such a practice would eliminate the

summer celery, which has not proved profitable, and might aid in lowering the percentage of infection on the autumn celery. When weeds become dry in the cultivated areas during the summer, enormous numbers of winged aphids fly into the celery fields and spread the virus of western celery mosaic to summer celery.

Reservoirs of Virus.—The natural host range of western celery mosaic among economic plants so far determined includes carrots and celeriac. Celery should not be planted adjacent to carrots or celeriac.

No weed hosts of the virus of western celery mosaic have been found under natural conditions up to the present time. The extracts from many weeds with mosaic symptoms have been inoculated in healthy celery, but all efforts to find a weed reservoir of the western-celery-mosaic virus were failures. Since transmission of the virus from celery can be accomplished more readily by aphids than by mechanical inoculation of diseased juice, further investigations on the weed host range have been undertaken. Observations indicate that there is usually a higher percentage of diseased celery along the margin of the celery fields adjacent to weeds.

Weed Eradication.—The eradication of weeds in and surrounding celery fields will reduce the population of aphids. Poison hemlock or spotted parsley (*Conium maculatum*), a tall, rank, poisonous, much-branched herb, abundant in the Santa Clara Valley, is one of the most favorable breeding plants of the honeysuckle aphid (*Rhopalosiphum melliferum*), and enormous populations developed on it. The rusty-banded aphid (*Aphis ferruginea-striata*) also breeds on it. It has been demonstrated to be naturally infected with three virus diseases of celery—yellow spot, ringspot, and California aster yellows (fig. 9), hence the importance of its eradication in the vicinity of celery fields. One grower sprayed this weed with oil to destroy it in the vicinity of his celery field.

The following paragraph on the distribution of poison hemlock is quoted from Sampson and Malmstem (*26*):

> Poison hemlock, although indigenous to Europe and Asia, has spread until it is widely distributed throughout California and the northwestern United States. It is confined almost wholly to waste places, growing on moist, shady, or fairly dry ground, in fields and canyons, and along dusty roadsides. It is in no way semiaquatic like water hemlock. Although primarily a low-altitude species, the range in elevation is from sea level to 7,500 feet.

Sweet fennel (*Foeniculum vulgare*), a perennial of short duration, cultivated as an annual or biennial, common in vacant fields and roadsides, is a favorable breeding plant of the celery aphid (*Aphis apii*), rusty-banded aphid, and the yellow willow aphid (*Cavariella capreae*).

It can be controlled by hoeing off the stems two or three times a season as near the surface of the ground as possible (*33*).

Roguing.—When a low percentage of western celery mosaic appears in the fields, some growers practice roguing of infected plants to pre-

Fig. 9.—Poison hemlock (*Conium maculatum*) naturally infected with California aster yellows, showing twisted petioles (Alvarado, March 3, 1936).

vent the spread of the disease by aphids. One grower collected the diseased plants in a large basket and destroyed them by burning with oil. It is evident, however, that aphids can recover the virus from infected plants before the earliest symptom of the disease develops.

Abandoned Mosaic-Celery Fields.—Celery fields which are not worth harvesting owing to western celery mosaic should be plowed under as soon as possible. The abandoned fields if not destroyed are a menace to neighboring fields as a source of virus. All fields should be plowed shortly after cutting celery so that no abandoned diseased celery plants remain after harvesting is completed.

Spraying.—The spray programs have been conducted by the growers, and since no unsprayed check or control plots were used, no statement can be made about the value of the sprays used to control aphids in relation to western celery mosaic. One grower employed three applications of a combination spray on celery seedlings grown in flats in the greenhouse, with the following proportions of ingredients:

6–8 pounds bordeaux
1 pint nicotine sulfate (Black Leaf 40)
100 gallons of water

In cool weather 8 pounds of bordeaux was used. The three applications of the spray were as follows:

1. One month after planting celery seeds.
2. Before transplanting celery seedlings in flats.
3. Before transplanting celery seedlings in the field.

Many growers in the Santa Clara Valley spray celery transplanted in the field with 2 or 3 applications of a combination spray consisting of bordeaux and nicotine sulfate to control late blight of celery (*Septoria apii*) and aphids. One grower used the combination spray alternating with either nicotine sulfate or the extract of pyrethrum at two-week intervals. It is believed that the extract of pyrethrum not only controls aphids but also the aster leafhopper (*Macrosteles divisus*), the most important leafhopper vector of celery-yellows virus (which is identical with the virus of California aster yellows).

The problem of aphid control in relation to western celery mosaic is complicated, and no definite statement can be made in regard to the value of a spray program up to the present time. The evidence presented in this paper shows that aphids which have not been found to breed on celery were capable of transmitting the virus of western celery mosaic. It is a well-known fact that when the pasture vegetation becomes dry during the spring on the uncultivated foothills, large flights of aphids occur in the cultivated areas. When weeds become dry in the cultivated areas during the summer, large populations of winged aphids have been collected in celery fields. Many of the aphids which have been reared on celery breed on a large number of other host plants, as recorded by Essig (7) in the preceding paper. It must also be noted that the erigeron root aphid (*Aphis middletonii*) and the rusty-banded aphids are root-feeding forms which cannot be controlled by spraying the foliage of celery.

Cold Frames.—Some growers remove the flats of celery seedlings from the greenhouse and allow the plants to harden out of doors for several weeks before transplanting in the field. Different species of aphids, as well as western-celery-mosaic infection, were found on celery seedlings

grown in flats and kept out of doors. The flats of celery seedlings should be placed in cold frames covered with muslin.

Some growers plant celery seeds in beds out of doors. An examination of celery seed beds showed the presence of aphids and of mosaic plants. Celery seedling should be grown in cold frames where small acreages are transplanted.

Dissemination.—Western celery mosaic does not occur in the San Joaquin Valley, and no celery seedlings unless grown outside of an infected district should be shipped into this valley. Although western celery mosaic is a serious disease in the Fog Belt of California, it is known to thrive in the hot interior regions such as the Sacramento Valley. The rusty-banded aphid, one of the most important carriers of the western-celery-mosaic virus, is known to occur in the San Joaquin Valley.

Celery was shipped from Florida to California and was transplanted in the field during 1936 in the Salinas Valley for seed production. Celery has also been shipped from Florida to growers in the Santa Clara Valley, but up to the present time southern celery mosaic is not known to occur in California.

DISCUSSION

A comparison of the host ranges of southern- and western-celery-mosaic viruses indicates that the two viruses are not identical. Inoculation experiments demonstrated that the southern-celery-mosaic virus may infect 91 different host plants, comprising 23 families of plants. Of the susceptible host plants, 46 have been found naturally infected in the field (*40*). Host-range studies of the western-celery-mosaic virus indicate that susceptible host plants are limited to plants of the family Umbelliferae. Carrots (*Daucus Carota* var. *sativa*) and celeriac (*Apium graveolens* var. *rapaceum*) are susceptible to both southern and western celery mosaic, but Hollow Crown and Long Smooth parsnips (*Pastinaca sativa*), susceptible to the former, are immune to western celery mosaic.

A comparison of the properties of the viruses of southern and western celery mosaic shows that the two viruses are distinct. Wellman (*36*) found that the extract from southern celery mosaic was infective after treatment at 65° C for 10 minutes, and occasional samples of viruliferous juice from tobacco and cucumber plants infected with southern celery mosaic were infective at 75°, but in all cases the virus was inactivated at 80°. The virus of western celery mosaic remained infective after heating the expressed juice at 55° for 10 minutes but was inactivated at 60°.

Wellman (*36*) produced infections with the following dilutions from plants infected with southern celery mosaic: celery 1:1,000, tobacco 1:10,000, and cucumber 1:100,000. The tolerance to dilution of the virus in juice extracted from western-celery-mosaic plants was 1:4,000.

Wellman (*36*) considers the virus causing southern celery mosaic a new one and has given it the designation "celery virus 1." Southern celery mosaic is similar in some ways to cucumber mosaic (cucumber virus 1, Doolittle) described by Doolittle (*3*), Johnson (*14*) and Doolittle and Walker (*4*) in host and symptomatological relations and in properties. The thermal inactivation of southern-celery-mosaic virus is only 5° C higher than the cucumber-mosaic virus. The southern-celery-mosaic virus, however, withstands aging *in vitro* from 6 to 8 days whereas the cucumber-mosaic virus withstands the treatment only about 3 days.

The virus causing southern celery mosaic should be designated as a strain of cucumber mosaic.

The evidence presented in this paper shows that the viruses of southern and western celery mosaics are not identical. There is no evidence to show that the virus of western celery mosaic is a strain of cucumber mosaic. The virus causing western celery mosaic is new; a description follows:

DESCRIPTION OF WESTERN-CELERY-MOSAIC VIRUS

Name: Western celery mosaic.[6]

Host family: Umbelliferae.

Symptoms of disease: On celery, vein clearing, followed by mottling, necrotic spotting, white spots or streaks on petioles, stunting of plant.

Incubation period of disease: 10 to 16 days or longer out of doors.

Property studies: Filterable through all grades of Chamberland filters, thermal inactivation 60° C in 10-minute exposure, tolerance to dilution 1:4,000, resistance to aging *in vitro* 7 days, resistance to 30 per cent alcohol supernatant liquid 1 hour, 40 per cent alcohol precipitate 1 hour.

Modes of transmission: mechanical inoculation with expressed juice, in nature by 11 species of aphids which breed on celery, *no specific aphid vector.*

SUMMARY

The following virus diseases of celery occur under natural conditions in California: western celery mosaic, celery calico, celery yellow spot, celery crinkle-leaf, celery yellows (the virus is identical with California aster yellows), and spotted wilt. Celery has been experimentally infected with the viruses of sugar-beet curly top and poison hemlock ringspot.

The host range of western celery mosaic is limited to the family Umbelliferae, to which celery belongs. The following economic plants have been demonstrated to be naturally infected with western celery mosaic up to the present time: varieties of celery (*Apium graveolens* var. *dulce*), celeriac (*Apium graveolens* var. *rapaceum*), and varieties of carrots

[6] Smith (*34*) classifies the western-celery-mosaic virus as a synonym of Apium Virus 1, Severin and Freitag.

(*Daucus Carota* var. *sativa*). The host range as determined by experimental infection, by juice inoculation and by infection by aphids consists of the following economic plants: Large Smooth Prague celeriac (*Apium graveolens* var. *rapaceum*), dill (*Anethum graveolens*), Curled chervil (*Anthriscus Cerefolium*), caraway (*Carum carvi*), coriander (*Coriandrum sativum*), varieties of carrots (*Daucus Carota* var. *sativa*) and Single or Plain parsley (*Petroselinum hortense*).

Mechanical inoculations of healthy celery plants with the juice from the leaves of mosaic carrots resulted in lower percentages of infections than those with juice from the roots.

The virus was more readily recovered from symptomless carriers of Single or Plain parsley by mechanical inoculation (42.9 per cent) than by the rusty-banded aphid (*Aphis ferruginea-striata*) (5.7 per cent).

Mechanical inoculation of cucumber plants with the extract from celery infected with western celery mosaic collected in 23 localities of California, and attempts to transmit the virus by 11 species of aphids from naturally infected celery were failures.

Some of the properties of the virus are summarized as follows: The virus of western celery mosaic passed through all grades of Chamberland filters. The thermal inactivation of the western-celery-mosaic virus was 60° C in 10-minute exposures. Freezing juice extracted from naturally infected celery kept in cold storage at —18° C did not inactivate the virus after 18 months. The tolerance to dilution of extracted diseased celery juice was 1:4,000. An inactivation of the virus occurs after extracted diseased celery juice was exposed to the air at room temperature for a period of 7 days. The western-celery-mosaic virus in the supernatant liquid was capable of withstanding treatment with 30 per cent alcohol and the precipitate with 40 per cent alcohol for 1 hour.

Six species of aphids which have not been found to breed on celery under field conditions were capable of transmitting the virus of western celery mosaic (table 12, p. 520).

Eleven species of aphids which breed on celery under natural conditions transmitted the virus of western celery mosaic; there is no *specific aphid vector* of the virus. A summary of the percentages of infections obtained with the different species is given in table 16, page 528.

The transmission of the virus by 11 species of aphids from naturally infected to healthy celery plants varied from 2.2 per cent to 92.5 per cent and by mechanical inoculation of juice extracted from the same naturally infected plants on which the aphids were reared averaged 48.2 per cent (table 15, p. 527) and in another experiment 53.8 per cent (table 4, p. 514).

The highest percentage of infections by single winged aphids was 7.0, produced by the celery-leaf aphid (*Aphis apigraveolens*) and by single wingless mature aphids 37.3, produced by the rusty-banded aphid (*A. ferruginea-striata*).

Ten species of aphids transmitted the virus from diseased to healthy celery plants during the first day, but 56 lots of 20 aphids tested had lost the infective power by the second day.

Five lots of 20 rusty-banded aphids (*Aphis ferruginea-striata*) infected the first set of healthy celery plants on which they were kept for a period of 12 hours, but when transferred hourly to successive sets of plants for a period of 8 hours, no infections occurred.

The retention of the virus by single infective wingless aphids varied from 1 to 8 hours and by lots of 20 infective aphids from 1 to 10 hours.

In some instances, aphids recovered the virus from celery infected with western celery mosaic before symptoms of the disease developed, in some on the same day after the earliest symptoms of the disease appeared, and in others in from 1 to 6 days after the first symptoms of the disease developed.

ACKNOWLEDGMENTS

The assistance of nontechnical employees of the W.P.A. is acknowledged.

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APPENDIX TO CITATIONS

Brief notes of the occurrence of celery mosaic in the United States have appeared from time to time in the *Plant Disease Reporter*.[7] Frequently the collaborators of these reports were not mentioned, and it was found more convenient to list them in the chronological order rather than under the names of collaborators and editors.

41. The Plant Disease Bulletin Suppl. **3**:108. 1919.
42. The Plant Disease Bulletin Suppl. **22**:406. 1922.
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55. The Plant Disease Reporter Suppl. **86**:56. 1935.
56. The Plant Disease Reporter Suppl. **90**:82. 1935.
57. The Plant Disease Reporter **19**:106. 1935.
58. The Plant Disease Reporter Suppl. **96**:193. 1936.
59. The Plant Disease Reporter **21**:77–79. 1937.

[7] A mimeographed pamphlet issued by the United States Department of Agriculture, Bureau of Plant Industry. Early issues of this publication appeared under the name *Plant Disease Bulletin*.

PLATES

Plate 1.—Celery calico: *A*, leaflets from a plant infected with the virus by mechanical inoculation, showing cleared veinlets and intervenal yellowing; *B*, faint discoloration, which was amber-yellow, near the basal region of celery leaflets, from a plant infected with the virus by the rusty-banded aphid (*Aphis ferruginea-striata*); *C*, bands, which were amber-yellow, near the margin of celery leaflets; from a plant infected with the virus by the honeysuckle aphid (*Rhopalosiphum melliferum*); *D*, a later stage showing green islands in the lemon-yellow areas of the leaflets, a reliable symptom of the disease on the outer leaves; *E*, green areas surrounded by chlorotic rings resembling ringspot; *F*, an advanced stage of the disease on the older leaves, showing green and yellow zigzag bands and many small green islands.

Plate 2.—*A* and *B*, Celery yellow spot: *A*, numerous chlorotic spots on the leaflets from a plant naturally infected with the disease (Milpitas, June 13, 1935); *B*, yellow stripes or bands along the veins from a plant naturally infected with the disease (Hollister, November 21, 1935). *C*, Leaflets from a plant experimentally infected with celery-crinkle-leaf virus showing cleared veinlets in chlorotic areas. *D*, Leaflets showing crinkling and blisterlike elevations. *E* and *F*, Poison-hemlock ringspot on celery leaflets; *E*, small chlorotic rings enclosing green spots; *F*, large irregular green areas surrounded by alternating yellow and green lines.

Plate 3.—*A* to *D*, Western celery mosaic: *A*, petioles showing white spots from a plant naturally infected (Milpitas, June 13, 1935); *B*, petioles showing longitudinal white streaks from plants experimentally infected by the cotton or melon aphid (*Aphis gossypii*); *C*, *D*, leaflets from plants naturally infected showing cleared veins and veinlets and puckering (Mountain View, October 16, 1934). *E*. Epidermis removed from three petioles, showing brown specks along the veins from a plant naturally infected with celery yellow spot (Milpitas, November 18, 1934, courtesy of M. W. Gardner).

Plate 4.—Western celery mosaic: *A*, leaflets from a naturally infected plant, showing small irregular dark areas, which were green, scattered in the light region, which was lemon yellow; *B*, leaflets showing somewhat larger irregular dark areas containing chlorophyll (Milpitas, July 17, 1935); *C*, leaflets from a naturally infected plant showing large dark irregular areas, which were green; *D*, leaflets showing large areas in which the chlorophyll was absent, with the margins and a few irregular dark areas containing chlorophyll (Gardena, July 1, 1935); *E*, leaflets from a naturally infected plant, showing dark margins containing chlorophyll and yellow areas (shown as white) devoid of chlorophyll; *F*, leaflets showing areas in which chlorophyll was present and absent (Milpitas, July 17, 1935).

Plate 5.—Western celery mosaic: *A*, brown necrotic spots on the upper surface of celery leaflets from a plant naturally infected (Gardena, July 1, 1935); *B*, brown necrotic areas covering most of the celery leaflets from a plant experimentally infected by mechanical inoculation; *C*, carrot (*Daucus Carota* var. *sativa*) leaflets from Danvers Half Long variety infected by the rusty-banded aphid (*Aphis ferruginea-striata*), showing chlorotic areas; *D*, *E*, carrot leaflets showing mottling from a plant naturally infected (Milpitas, June 10, 1936); *F*, curled chervil (*Anthriscus Cerefolium*) leaflets from a plant infected by the rusty-banded aphid, showing chlorotic areas and brown necrotic spotting.

Plate 6.—*A* to *C*, Western celery mosaic: *A*, celery leaf with all leaflets narrow with the exception of the apical leaflet, from a plant infected by the rusty-banded aphid (*Aphis ferruginea-striata*); *B*, portion of one leaflet narrow from a celery plant experimentally infected; *C*, malformed, twisted, thickened celery leaflets showing mottling, from a plant naturally infected (Gardena, July 1, 1935). *D*, Celery leaflets showing blisterlike pustules resembling cucumber mosaic on celery (Milpitas, April 10, 1935). *E*, Center, celery leaflets from a healthy plant; grouped around it are four linear leaflets resembling cucumber mosaic on celery, but cucumber mosaic was not transmitted to healthy celery and cucumber plants by juice inoculations (Milpitas, April 10, 1935). *F*, Narrow leaflets from a healthy plant.

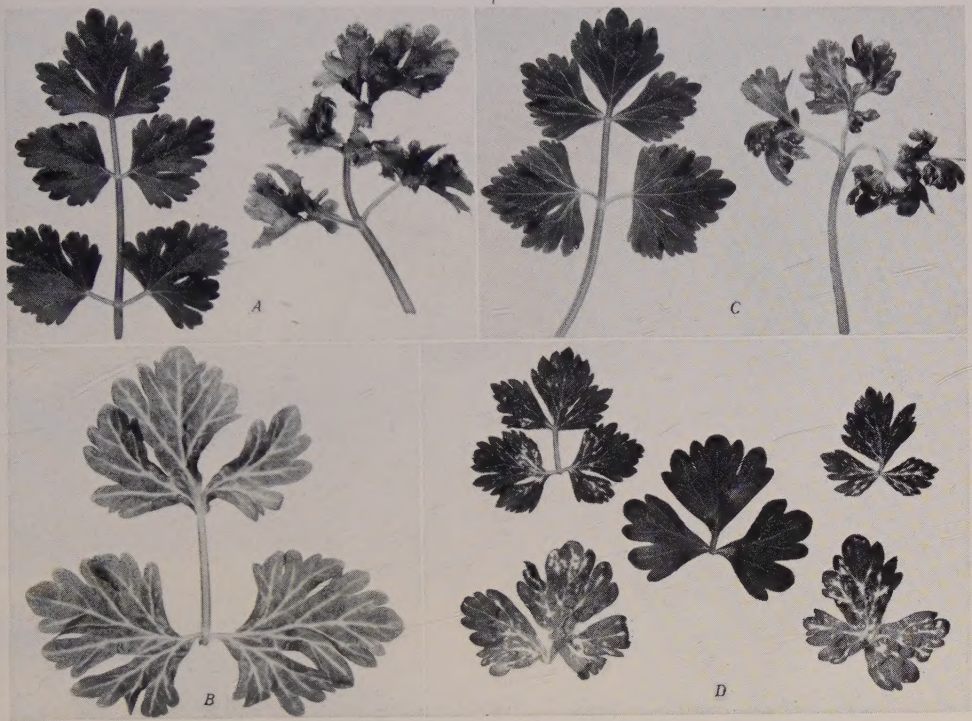

Plate 7.—*A*, Left, leaf from healthy celery plant; right, curled celery leaflets probably caused by feeding punctures of noninfective cotton or melon aphids (*Aphis gossypii*). *B*, Celery leaf showing cleared veins probably caused by saliva of noninfective yellow willow aphids (*Cavariella capreae*). *C*, Left, leaf from healthy celery plant; right, curled celery leaflets probably caused by feeding punctures of noninfective foxglove aphid (*Myzus convolvuli*). *D*, Center, leaflets from healthy celery plant; grouped around it are four celery leaflets showing yellow spots or streaks along the veins, probably caused by the saliva of noninfective foxglove aphid.

Plate 8.—Coriander (*Coriandrum sativum*): upper left, leaf from check or control plant; upper right, leaf from a plant infected with western celery mosaic showing cleared veinlets; lower, leaves showing mottling.